

SEASONAL FOOD WEB MODELS FOR THE OREGON INNER-SHELF ECOSYSTEM: INVESTIGATING THE ROLE OF LARGE JELLYFISH

JAMES J. RUZICKA

Cooperative Institute for Marine Resources Studies
Oregon State University
2030 SE Marine Science Drive
Newport, Oregon 97365
Jim.Ruzicka@noaa.gov

RICHARD D. BRODEUR AND THOMAS C. WAINWRIGHT

National Oceanic and Atmospheric Administration
Northwest Fisheries Science Center
Fisheries Ecology Division
2030 SE Marine Science Drive
Newport, Oregon 97365

ABSTRACT

We developed two seasonal food-web models, spring and summer, within the Ecopath framework for the Oregon upwelling ecosystem to investigate the role of large jellyfish as competitors for zooplankton prey. We used information about fish and jellyfish biomass, distribution, and diet derived from pelagic trawl survey data. Information about lower trophic-level production was acquired from zooplankton survey data. The models indicate that in spring, jellyfish are a modest consumer of zooplankton, and forage fishes dominate the system in terms of biomass and consumption. By late summer, jellyfish become the major zooplankton consumers, and they consume 17% of the summer zooplankton production while forage fish consume 9%. Jellyfish appear to divert zooplankton production away from upper trophic levels. Only 2% of the energy consumed by jellyfish is passed to higher trophic levels. However, the role of jellyfish as competitors may be moderate; a large proportion of zooplankton production (40%–44%) is not consumed but lost to detritus.

INTRODUCTION

The northern California Current (NCC) off Oregon and Washington supports a seasonally productive and open ecosystem. Upwelling-favorable winds dominate along the Oregon and Washington coasts after the spring transition during March or April, and continue through October or November when downwelling conditions normally occur (Strub et al. 1987). During the upwelling season, the NCC is home to a diverse pelagic fish community, including the juveniles of important salmon stocks, resident species such as anchovies, smelts, and herring, and transient species migrating from the south such as sardines, hake, and mackerels (Brodeur et al. 2005). Ecosystem productivity and food-web structure vary on seasonal-to-decadal time scales due to the timing and strength of seasonal alongshore winds and forcing by basin-scale physical processes (e.g., El Niño, Pacific Decadal Oscillation) and longer-term climate trends (Batchelder et al. 2002). These variations affect the survival and productivity of all members of the pelagic community in the NCC.

Jellyfish biomass has increased dramatically in many ecosystems around the world in the past two decades (Mills 2001; Brodeur et al. 2002; Kawahara et al. 2006; Attrill et al. 2007). Jellyfish have several characteristics that place them in a unique and influential position within an ecosystem, which can have negative effects upon pelagic fish: high rates of reproduction and growth, generally broad diets that can overlap with planktivorous fish, and few predators. Increases in jellyfish biomass are generally accompanied by decreases in fish biomass (e.g., Lynam et al. 2006), which suggests substantial fish–jellyfish interactions that may affect fish growth, survival, and distribution. Thus, there is a recognized need to understand the role of jellyfish in pelagic ecosystems, the causes of jellyfish proliferation, and the potential consequences to ecosystem functioning and to fisheries when jellyfish biomass blooms. Jellyfish may have a negative impact upon pelagic fishes as both predators and competitors (Purcell and Arai 2001). Jellyfish, in particular, can obtain a high biomass and may become an important energy pathway diverting zooplankton production away from pelagic fishes (Mills 1995, 2001; Lynam et al. 2006).

Here, we examine the role of jellyfish in the NCC upwelling ecosystem off the Oregon coast. Jellyfish represent a major portion of the pelagic biomass in the NCC (Shenker 1984; Suchman and Brodeur 2005), although neither their long-term trends in biomass nor their trophic role in the ecosystem has been well studied. Suchman et al. (in press) examined the diet of several dominant jellyfish in this region and compared their consumption to available zooplankton. They found that these species can have a major impact on production of several zooplankton taxa. Brodeur et al.¹ compared the diets and distribution of these jellyfish to those of co-occurring pelagic fishes and found that the potential for competitive interactions can be substantial due to high dietary and spatial overlap.

The goals of this study are to: (1) develop two mass-

¹Brodeur, R. D., C. L. Suchman, D. C. Reese, T. W. Miller, and E. A. Daly. Submitted-a. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. *Mar. Biol.* NOAA/NMFS/NWFSC, Newport, Oregon.

balance food-web models of the northern California Current upwelling ecosystem with focus upon the pelagic sub-system using data from large-scale surveys for biomass, distribution, seasonal patterns of biomass change, and local and contemporary diet information, (2) investigate change in trophic structure during the early (spring) and late (summer) upwelling season, and (3) investigate the importance of large jellyfish within the northern California Current upwelling ecosystem, their impact on lower trophic levels, their importance as competitors with planktivorous fishes, and their impact upon higher trophic levels.

MATERIALS AND METHODS

Model Overview

Two seasonal-scale food-web models have been developed for the inner-shelf of the Oregon upwelling ecosystem within the Ecopath framework (Christensen and Walters 2004). The models represent the spring (April-June) and summer (July-September) periods for a composite of the years 2000 and 2002; these are the most recent years during which pelagic fish surveys were conducted over the full North-South extent of the Oregon shelf. The models' domain extends from 46°N to 41.8°N (southern Oregon border) and excludes the mouth of the Columbia River which has its own distinct and important physical and ecological characteristics (Hickey and Banas 2003). Offshore, the models extend to the 125 m isobath, encompassing an area of approximately 9,650 km².

Ecopath is a software package for synthesizing diet, production, and metabolic information into a mass-balanced system of interactions between all trophic groups that define an ecosystem (Christensen and Walters 2004). The Ecopath master equation allocates the productivity of each trophic group to fishery harvest, transfer to higher trophic level via predation, emigration out of the ecosystem, growth, and other mortality (e.g., senescence):

$$B_i \cdot (P/B)_i - \sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji} - (P/B)_i \cdot B_i \cdot EE_i - Y_i - E_i - BA_i = 0 \quad (1)$$

where, for each trophic group (*i*), *B* is the biomass, *P/B* is the mass-specific production rate, *Q/B* is the mass-specific consumption rate, *DC_{ji}* is the fraction of prey (*i*) in the diet of predator (*j*), *Y* is the fishery harvest rate, *E* is the emigration rate, *EE* is the ecotrophic efficiency (the fraction of production consumed within the system), and *BA* is the biomass accumulation rate. The term:

$$\sum_{j=1}^n B_j \cdot (Q/B)_j \cdot DC_{ji}$$

is the total predation mortality rate, and the term $(P/B)_i \cdot B_i \cdot EE_i$ is the non-predation mortality rate (Christensen and Walters 2004). As input parameters for each trophic group, Ecopath requires the weight-specific diet composition, the fishery harvest rate, and at least three of the following parameters: *B*, *P/B*, *Q/B*, or *EE*. As an assumption of steady-state community composition is not made in the seasonal models developed here, biomass change rate (*BA*) from endemic growth and mortality and emigration (or immigration) rates (*E*) are also required. Ecopath also accounts for the energy flow within individual trophic groups:

$$\text{consumption} = \text{production} + \text{respiration} + \text{egestion}, \quad (2)$$

where egestion is assumed to be 20% for all groups in the present models.

The two seasonal models presented here each consist of one producer group, 48 consumer groups, two egg groups, and three detritus groups. They are based upon the annual-scale northern California Current models developed by Field and colleagues within the Ecopath framework (Field 2004; Field and Francis 2005; Field et al. 2006). The benthic food web (trophic groupings, diet, physiological rate parameters) is modified from the Field models as are the marine mammal and seabird groups. The information required to develop the pelagic food web was obtained from a variety of sources: recent pelagic fish and plankton survey studies off Oregon, local diet information, fishery records, the literature, and other northeast Pacific food-web models.

Community Composition

BPA and GLOBEC pelagic trawl surveys: The composition of the pelagic nekton and jellyfish community on the Oregon shelf in spring and summer (2000 and 2002) was estimated from the Bonneville Power Administration (BPA) ocean salmon survey program and the GLOBEC pelagic survey program. The BPA ocean salmon survey sampled three transect lines in May, June, and September from 45.7°N to 44.6°N and from the 30 m isobath onto the continental slope. The GLOBEC survey consisted of four cruises (June 2000 and 2002, September 2000 and 2002) from 44.4°N to 42°N from the 30 m isobath onto the continental slope. Both survey programs quantitatively sampled the upper 20 m of the water-column using an 18 × 30 m Nordic Rope trawl during daylight hours. Detailed trawl and sampling protocol information for both programs are provided by Emmett et al. (2005). The combined sampling area is shown in Figure 1.

Total wet weights of individual species in each trawl

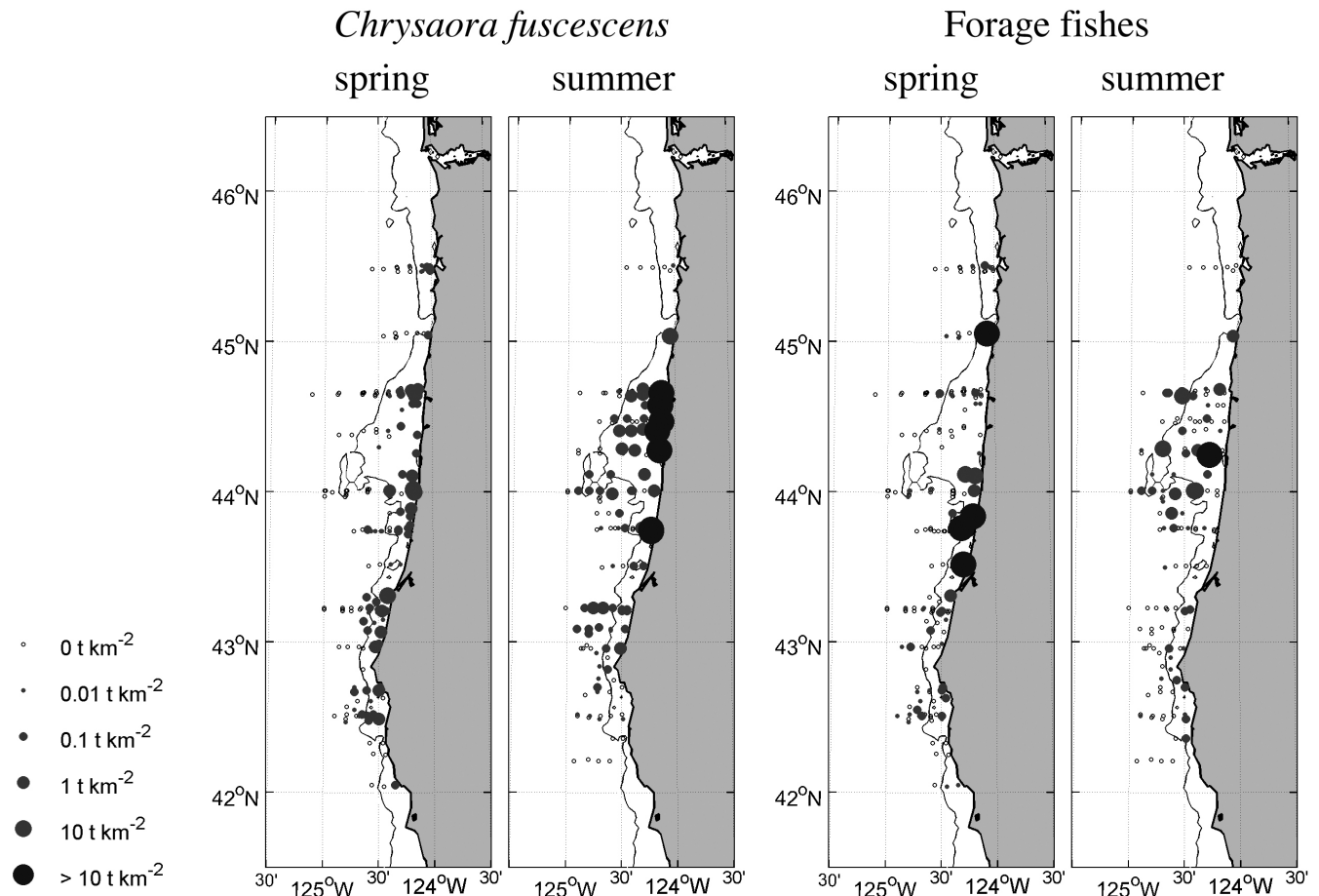


Figure 1. Spring and summer distribution of sea nettle jellyfish (*Chrysaora fuscescens*) and forage fishes (smelt, shad, sardine, herring, anchovy) off the Oregon coast sampled during the BPA and GLOBEC pelagic surveys in 2000 and 2002 (years pooled). Line indicates 125 m isobath.

were calculated from length-distribution data by applying species-specific empirical length-weight relations from the literature and FishBase (<http://www.fishbase.org>). Trawl data from years 2000 and 2002 were pooled to calculate the mean spring (141 trawls) and summer (103 trawls) areal density and biomass after the method of Pennington (1996) for survey data that include trawls with zero catch and non-zero trawls that are lognormally distributed. The areal biomass and density estimates for groups informed by the BPA and GLOBEC pelagic surveys and not adjusted for catchability are presented in Table 1 (see Appendix for details of pelagic fish biomass values used in models).

Newport Hydrographic line (NH-line): The seasonal biomasses of phytoplankton, copepods, and euphausiids were estimated from time-series data collected along the Newport Hydrographic line (NH-line) across the central Oregon shelf (44.67°N). The phytoplankton and copepod biomass values used in the models are the spatial and seasonal mean values observed during bi-weekly surveys at stations NH-05 (60 m), NH-10 (80 m), and NH-15 (90 m) in the spring and summer seasons of 2000

through 2004 (W. T. Peterson et al., NOAA/NMFS, Newport, Oregon, unpub. data). See Appendix for details and Table 2.

BPA zooplankton survey: Information about larval euphausiids, fish eggs, pelagic amphipods, and individual macro-zooplankton groups was provided by zooplankton surveys conducted as part of, and at the same stations as, the BPA ocean salmon survey in northern Oregon and Washington (C. Morgan, OSU, Newport, Oregon, unpub. data). Zooplankton were collected using a 1 m, 335 μ m mesh ring-net towed obliquely from 20–30 m to the surface at 3.7 km/h. The detailed laboratory protocol is described by Schabetsberger et al. (2003). Total wet weights of individual species in each tow were calculated from length-distribution data by applying species-specific empirical length-weight or length-carbon relations (from the literature and W. T. Peterson et al., NOAA/NMFS, Newport, Oregon, unpub. data) and assuming dry:wet weight = 0.19 (Omori 1969). Areal biomass estimates for zooplankton groups measured during the BPA/GLOBEC zooplankton survey and not adjusted for biomass below the tow depth are

TABLE 1

Areal density and biomass of pelagic fishes and jellyfish as estimated from GLOBEC and BPA pelagic trawl surveys over the Oregon inner-shelf during the spring and summers of 2000 and 2002. Estimates are derived from 141 spring trawls and 103 summer trawls. Both survey years are pooled. These estimates are unadjusted for catchability.

Group	SPRING		SUMMER	
	biomass (t/km ²)	density (ind./km ²)	biomass (t/km ²)	density (ind./km ²)
Forage fishes				
smelt	0.0181	24,544	0.0086	8,569
shad	<0.0001	44	0.0001	54
sardine	0.0421	7,990	0.2514	251,405
herring	0.4088	1,157,243	0.0635	39,763
anchovy	0.0001	85	0.0001	130
saury	<0.0001	8	0.0007	742
Jellyfish				
sea nettle	0.0646	690	1.5723	2,282,936
moon jelly	0.0791	800,732	0.5115	919,137
egg-yolk jelly	0.0041	15,110	0.0716	71,630
water jelly	0.0421	37,531	0.0241	33,509
Salmon				
coho	0.0104	106,655	0.0214	21,427
Chinook	0.0587	445,669	0.0448	44,791
other salmon	0.0079	54,463	0.0001	97
juvenile salmon	0.0030	5,348	0.0089	24,910
Piscivorous fishes				
mackerels	0.0093	5	0.0859	49
sharks	0.0234	23,447	0.0106	10,609

TABLE 2

Areal density and biomass of zooplankton as estimated from NH-Line and BPA zooplankton surveys over the Oregon and Washington inner shelf during the spring and summers of 2000 and 2002. Values presented here are un-scaled to account for biomass beneath the tow depth. See Appendix for details on biomass estimations used in models.

Group	SPRING		SUMMER	
	biomass (t/km ²)	density (ind./km ²)	biomass (t/km ²)	density (ind./km ²)
phytoplankton ^a	26.9923	—	74.2414	—
copepods ^a	12.8749	—	17.6110	—
<i>Euphausia pacifica</i> (adult) ^b	0.7082	4.31·10 ⁷	6.9833	2.67·10 ⁸
<i>Thysanoessa spinifera</i> (adult) ^b	1.1739	7.70·10 ⁶	6.4549	7.27·10 ⁷
euphausiid (larvae) ^c	0.0554	4.51·10 ⁸	0.1405	7.22·10 ⁸
euphausiid (eggs) ^d	0.2223	4.05·10 ⁹	0.0010	1.85·10 ⁷
pelagic amphipods ^c	0.0096	4.45·10 ⁶	0.0170	4.69·10 ⁶
meroplankton ^c	0.1398	6.70·10 ⁸	0.0479	1.60·10 ⁹
chaetognaths ^c	0.0417	9.80·10 ⁷	0.0691	1.44·10 ⁸
pteropods ^c	0.0083	1.08·10 ⁸	0.0076	1.15·10 ⁸
ichthyoplankton ^c	0.0028	1.50·10 ⁶	0.0005	1.42·10 ⁶
fish eggs ^d	0.2032	1.39·10 ⁸	0.0237	1.73·10 ⁷

^aNH-line (mean 2000–2004, NH-05, NH-10, NH-15) (W. T. Peterson, NOAA/NMFS, Newport, Oregon, unpub. data)

^bNH-line (median 2001–2004, NH-20) (T. Shaw, OSU, Newport, Oregon, unpub. data)

^cBPA (Oregon & Washington; 2000 & 2002 pooled; 43 spring tows, 36 summer tows) (C. Morgan, OSU, Newport, Oregon, unpub. data)

^dBPA (Oregon; 2000 & 2002 pooled; 13 spring tows, 6 summer tows) (C. Morgan, OSU, Newport, Oregon, unpub. data)

presented in Table 2 (see Appendix for details of zooplankton biomass values used in models).

NOAA West Coast bottom trawl survey: Information about the summer abundance of demersal fishes and hake was provided by the 2001 NOAA West Coast bottom trawl survey (Weinberg et al. 2002). The coast-wide survey was organized latitudinally into five statistical areas defined by the International North Pacific Fisheries Commission (INPFC) and cross-shelf into three depth strata. Survey biomass data is reapportioned into the Oregon inner-shelf model domain using a strategy in which the biomass of all INPFC areas and depth strata that overlap the model domain are scaled by the fractional area of overlap and summed. Bottom trawl surveys are limited in their ability to accurately survey semipelagic species (e.g., hake, some rockfish species) and do not sample inshore of the 55 m isobath. Our efforts to account for these limitations for individual trophic groups are detailed in the Appendix.

Trophic Group Parameters

The definitions and the parameter details of individual trophic groups are provided in the Appendix. Physiological rate parameters, production (P/B), consumption (Q/B), and growth efficiency (P/Q), were obtained from the literature, other ecosystem models, or calculated from local and contemporary data.

Production rate parameters (P/B) were calculated for juvenile salmon and carnivorous jellyfish based on data from the BPA and GLOBEC mesoscale surveys and local observations of jellyfish growth rates (Suchman and Brodeur 2005). Physiological parameters of zooplankton and pelagic fishes were obtained from the literature and other Northeast Pacific models (e.g., Pauly and Christensen 1996; Aydin et al. 2003; Preikshot 2005). Parameters for demersal fishes, seabirds, and mammals came from Field (2004).

Biomass accumulation rates (BA) were calculated as the change in the seasonal mean biomass from the spring to the summer. For most plankton groups, BA was attributed to local net production (but see Appendix for euphausiids). For other groups, BA was attributed partially to local net production and partially to migration. For forage fishes, 10% of the local production (calculated from P/B) contributes to BA . For salmon and sharks, BA was attributed entirely to migration. For dogfish, mackerel, and hake, BA was attributed entirely to migration in the spring and partially to net production in the summer. For juvenile salmon, BA was attributed entirely to migration in the spring (smolts entering from rivers) and entirely to net local production in the summer.

The parameter set for the balanced spring and summer food-web models are presented in Table 3 and include parameters estimated by Ecopath: trophic level

TABLE 3

Parameter-set for the balanced spring and summer food-web models for the Oregon inner-shelf ecosystem. Underlined values are estimated by the model. P/B = production rate, Q/B = consumption rate, P/Q = gross growth efficiency, B = biomass, TL = trophic level, EE = ecotrophic efficiency, BA = biomass accumulation rate, EM = spring emigration rate (summer emigration rate in parentheses if different).

	SPRING MODEL						SUMMER MODEL				
	P/B per yr	Q/B per yr	P/Q	B t/km ²	TL	EE	B t/km ²	TL	EE	BA t/km ² /yr	EM t km ⁻² yr ⁻¹
phytoplankton	180	—	—	26.989	<u>1.00</u>	<u>0.48</u>	74.244	<u>1.00</u>	<u>0.26</u>	187.480	0.000
copepods	37	148	0.25	12.875	<u>2.00</u>	<u>0.50</u>	17.611	<u>2.00</u>	<u>0.50</u>	18.791	0.000
<i>E. pacifica</i> (adult)	5.8	23.2	0.25	0.709	<u>2.08</u>	<u>0.78</u>	6.984	<u>2.08</u>	<u>0.85</u>	24.895	-24.895
<i>T. spinifera</i> (adult)	7	28	0.25	1.174	<u>2.08</u>	<u>0.95</u>	6.455	<u>2.08</u>	<u>0.94</u>	20.951	-16.760
euphausiid (larva)	69.8	279.2	0.25	0.055	<u>2.00</u>	<u>0.82</u>	0.141	<u>2.00</u>	<u>0.92</u>	0.338	0.000
pelagic amphipods	7	28	0.25	<u>1.965</u>	<u>2.05</u>	0.90	<u>1.426</u>	<u>2.05</u>	0.90	0.000	0.000
macro-zooplankton	7	28	0.25	<u>4.063</u>	<u>2.67</u>	0.90	<u>6.474</u>	<u>2.67</u>	0.90	0.000	0.000
small jellyfish	9	30	0.3	<u>3.078</u>	<u>2.00</u>	0.90	<u>8.945</u>	<u>2.00</u>	0.90	0.000	0.000
large jellyfish	15	60	0.25	0.855	<u>2.80</u>	<u>0.86</u>	3.269	<u>2.80</u>	<u>0.29</u>	9.581	0.000
pandalid shrimp	3	12	0.25	<u>1.052</u>	<u>2.69</u>	0.90	<u>4.062</u>	<u>2.70</u>	0.90	0.000	0.000
benthic shrimp	3	12	0.25	<u>2.019</u>	<u>3.06</u>	0.90	<u>4.405</u>	<u>3.06</u>	0.90	0.000	0.000
Dungeness crab	1	4	0.25	2.649	<u>3.27</u>	<u>0.21</u>	2.649	<u>3.24</u>	<u>0.20</u>	0.000	0.000
epifauna	3	12	0.25	<u>8.967</u>	<u>2.46</u>	0.90	<u>15.227</u>	<u>2.46</u>	0.90	0.000	0.000
infauna	3	12	0.25	<u>25.050</u>	<u>2.00</u>	0.90	<u>44.652</u>	<u>2.00</u>	0.90	0.000	0.000
cephalopod	3	12	0.25	<u>0.773</u>	<u>3.36</u>	0.90	<u>1.242</u>	<u>3.29</u>	0.90	0.000	0.000
smelt	2	8	0.25	0.904	<u>3.19</u>	<u>0.51</u>	0.428	<u>3.18</u>	<u>0.88</u>	-1.890	2.031
shad	2	8	0.25	0.002	<u>3.02</u>	<u>0.66</u>	0.003	<u>3.04</u>	<u>0.88</u>	0.002	-0.002
sardine	2	8	0.25	2.107	<u>2.69</u>	<u>0.69</u>	12.570	<u>2.70</u>	<u>0.77</u>	41.509	-40.338
herring	2.2	8.8	0.25	20.442	<u>2.66</u>	<u>0.34</u>	3.175	<u>2.62</u>	<u>0.89</u>	-68.502	70.545
anchovy	2	8	0.25	0.005	<u>2.64</u>	<u>0.75</u>	0.005	<u>2.64</u>	<u>0.94</u>	0.000	0.001
juvenile salmon	6.5	30	0.217	0.018	<u>3.75</u>	<u>0.49</u>	0.053	<u>3.69</u>	<u>0.92</u>	0.139	-0.139 (0.000)
juvenile rockfish	2	8	0.25	<u>0.699</u>	<u>3.18</u>	0.90	<u>2.255</u>	<u>3.18</u>	0.90	0.000	0.000
juvenile fish other	2	8	0.25	<u>2.994</u>	<u>2.98</u>	0.90	<u>5.523</u>	<u>2.91</u>	0.90	0.000	0.000
coho	2.5	16.5	0.152	0.063	<u>3.76</u>	<u>0.46</u>	0.129	<u>3.70</u>	<u>0.38</u>	0.263	-0.263
Chinook	0.75	5	0.15	0.352	<u>3.70</u>	<u>0.48</u>	0.269	<u>3.67</u>	<u>0.68</u>	-0.331	0.331
other salmon	1.9	14.5	0.131	0.047	<u>3.40</u>	<u>0.22</u>	0.001	<u>3.43</u>	<u>0.20</u>	-0.185	0.185
shark	0.2	5	0.04	0.023	<u>4.24</u>	<u>0.01</u>	0.011	<u>4.33</u>	<u>0.79</u>	-0.051	0.051
dogfish	0.1	2.5	0.04	0.177	<u>3.98</u>	<u>0.88</u>	0.237	<u>4.00</u>	<u>0.95</u>	0.238	-0.238 (-0.233)
mackerel	0.5	7	0.071	0.093	<u>3.33</u>	<u>0.80</u>	0.859	<u>3.32</u>	<u>0.23</u>	3.041	-3.041 (-3.012)
hake	0.8	5	0.16	1.815	<u>3.76</u>	<u>0.87</u>	13.659	<u>3.51</u>	<u>0.39</u>	44.568	-44.568 (-43.599)
mesopelagics	0.6	3	0.2	<u>1.938</u>	<u>3.08</u>	0.90	<u>2.349</u>	<u>3.13</u>	0.90	0.000	0.000
sablefish	0.09	2.1	0.043	2.589	<u>3.67</u>	<u>0.51</u>	2.589	<u>3.71</u>	<u>0.51</u>	0.000	0.000
lingcod	0.3	2.4	0.125	0.107	<u>4.23</u>	<u>0.89</u>	0.107	<u>4.21</u>	<u>0.81</u>	0.000	0.000
skates & rays	0.2	2	0.1	0.155	<u>3.97</u>	<u>0.93</u>	0.155	<u>3.95</u>	<u>0.71</u>	0.000	0.000
small benthic fishes	0.5	2.5	0.2	<u>2.539</u>	<u>3.35</u>	0.90	<u>3.469</u>	<u>3.35</u>	0.90	0.000	0.000
shelf piscivore rockfish	0.13	2.2	0.059	2.404	<u>3.77</u>	<u>0.90</u>	2.404	<u>3.61</u>	<u>0.87</u>	0.000	0.000
shelf planktivore rockfish	0.13	2.2	0.059	0.837	<u>3.20</u>	<u>0.83</u>	0.837	<u>3.21</u>	<u>0.90</u>	0.000	0.000
slope planktivore rockfish	0.08	2.1	0.038	0.080	<u>3.72</u>	<u>0.67</u>	0.080	<u>3.42</u>	<u>0.81</u>	0.000	0.000
flatfish (benthic feeder)	0.301	1.669	0.181	2.393	<u>3.18</u>	<u>0.84</u>	2.393	<u>3.18</u>	<u>0.88</u>	0.000	0.000
flatfish (water-column feeder)	0.345	2.008	0.172	0.533	<u>3.98</u>	<u>0.94</u>	0.533	<u>4.12</u>	<u>0.84</u>	0.000	0.000
flatfish (small)	0.5	2.5	0.2	1.774	<u>3.43</u>	<u>0.84</u>	1.774	<u>3.43</u>	<u>0.90</u>	0.000	0.000
alcids	0.1	129	0.001	0.009	<u>3.76</u>	<u>0.30</u>	0.009	<u>3.77</u>	<u>0.30</u>	0.000	0.000
gulls	0.12	122	0.001	0.002	<u>3.74</u>	<u>0.00</u>	0.002	<u>3.70</u>	<u>0.00</u>	0.000	0.000
shearwaters	0.1	138	0.001	0.014	<u>3.77</u>	<u>0.00</u>	0.021	<u>3.76</u>	<u>0.00</u>	0.027	-0.027
harbor seals	0.08	8.3	0.01	0.037	<u>4.17</u>	<u>0.00</u>	0.037	<u>4.22</u>	<u>0.00</u>	0.000	0.000
sea lions	0.07	17.4	0.004	0.032	<u>4.30</u>	<u>0.00</u>	0.032	<u>4.32</u>	<u>0.00</u>	0.000	0.000
gray whales	0.04	8.9	0.004	0.090	<u>3.44</u>	<u>0.00</u>	0.090	<u>3.44</u>	<u>0.00</u>	0.000	0.000
baleen whales	0.04	7.6	0.005	0.043	<u>3.27</u>	<u>0.00</u>	0.043	<u>3.31</u>	<u>0.00</u>	0.000	0.000
toothed whales	0.07	28.9	0.002	0.014	<u>4.18</u>	<u>0.00</u>	0.014	<u>4.20</u>	<u>0.00</u>	0.000	0.000
euphausiid eggs	—	—	—	0.077	<u>1.00</u>	<u>0.93</u>	0.468	<u>1.00</u>	<u>0.90</u>	0.000	0.000
fish eggs	—	—	—	0.203	<u>1.00</u>	<u>0.93</u>	0.024	<u>1.00</u>	<u>0.76</u>	0.000	0.000
pelagic detritus	—	—	—	9.072	<u>1.00</u>	<u>0.02</u>	9.072	<u>1.00</u>	<u>0.01</u>	0.000	0.000
fishery offal	—	—	—	9.072	<u>1.00</u>	<u>0.02</u>	9.072	<u>1.00</u>	<u>0.03</u>	0.000	0.000
benthic detritus	—	—	—	9.072	<u>1.00</u>	<u>0.11</u>	9.072	<u>1.00</u>	<u>0.06</u>	0.000	0.000

TABLE 4

Diet matrices for the spring and summer models. Values are wet weight percent (rounded to nearest whole percent) of each prey group (left column) in the diet of each predator group (top row). First value given is for the spring model, second value given is for the summer model when different, T = trace (<0.5%). Prey not shown are gulls, shearwaters, and mammals (groups 43–49) which have no predators in the models.

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 phytoplankton	100	90	90	100	15	33/34	75	43	29/23					50/41	36/25	92/62
2 copepods		8	8		5	55/46			1/3					2/13	2/1	3/19
3 <i>E. pacifica</i>						1/4			1/3					2/13	2/16	4/17
4 <i>T. spinifer</i>					T	T		5/4	T					T	T	
5 euphausiid-larvae									1					1	15	1
6 pelagic amphipod						2		3	3					12/10	20	T
7 macro-zooplankton						1		29							20	
8 small jellyfish						5										
9 large jellyfish						1/2										
10 pandalid shrimp														4/3		
11 benthic shrimp											20	1		3/2		
12 Dungeness crab											1					
13 epifauna									6	44	23	1		1	T	
14 infauna									25	40	40	42		T		1
15 cephalopod											T			2		
16 smelt											T					
17 shad																
18 sardine														1/2		
19 herring											2/1			13/3		
20 anchovy																
21 juvenile salmon														T		
22 juvenile rockfish											T			2		
23 juvenile fish										1	1			4	5/3	
24 coho																
25 chinook																
26 other salmon																
27 shark																
28 dogfish																
29 mackerel																
30 hake														5/4		
31 mesopelagics																
32 sablefish																
33 lingcod																
34 skates & rays																
35 benthic fish-small																
36 rockfish-piscivore											1					
37 rockfish-shelf plank.																
38 rockfish-slope plank.																
39 flatfish-benthic											T					
40 flatfish-water-column																
41 flatfish-small											1					
42 alcid																
50 euphausiid-eggs		2	2			1		21/22	1						T	
51 fish-eggs						1		T								
52 pelagic detritus					80	1	25									
53 fishery offal									35	15	2	1	100			
54 benthic detritus											9/11	55				

TABLE 4 (continued)
Diet matrices for the spring and summer models. Values are wet weight percent (rounded to nearest whole percent) of each prey group (left column) in the diet of each predator group (top row). First value given is for the spring model, second value given is for the summer model when different, T = trace (<0.5%). Prey not shown are gulls, shearwaters, and mammals (groups 43–49) which have no predators in the models.

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1 phytoplankton	38	38/44	38/40			11/18										
2 copepods	47/40	47/30	40/19	15/8	57/54	65/56			14/11			53/32		78/55		
3 <i>E. pacifica</i>	T/5	1/6	T/5	1/8	1/2	T/1	3/9	6/12	T/3		4/8	6/25	1/17	1/15	2/4	
4 <i>T. spinifera</i>	T/3	1/8	T/15	1/8	1/2	T/1	3/8	6/11	T/3		5/8	1/6	2/25	T/8	3/5	
5 euphausiid-larvae	T	T		T	T/1	T								T/1		
6 pelagic amphipod	1	4	T	2	8	2	1	1	16		T	1		5/3	T	
7 macro-zooplankton	12	7/6	5	6/5	25	10	15	5	2		3/0	10	8	5/6	T	
8 small jellyfish	1		15	2/1	6	4	1	1	25		3/2	1	0/1	7/6	5/4	
9 large jellyfish								T	1		4/2		11/13	1	2/4	1/2
10 pandalid shrimp						1					4/2	T	5/9		6	2
11 benthic shrimp										1	4/3				2/3	5/6
12 Dungeness crab						2					16/11				4	6
13 epifauna						1									2	
14 infauna															5	16/15
15 cephalopod			T	T			10	2/3	10/15	2	1	2	5/2	3/5	2	1
16 smelt				2/1			3/4	3	1	2/1	1/T	1/T	1/0		2/t	
17 shad				T				T/0								
18 sardine				1			5/20	6/25	2/10	4/15	2/8	2/7	4/11		3/12	1/5
19 herring				4/2			47/12	53/12	21/5	34/8	15/3	10/2	49/2		25/4	10/4
20 anchovy				1/T			0/T	T								
21 juvenile salmon										1	1	1	T		T	
22 juvenile rockfish				11		2	3/5	5	1/2	T	1	1/2	5/4		1	3
23 juvenile fish	T	1		54/53	2		10/15	13/16	4/5	1	3	11	6		2	3
24 coho										2/3						
25 chinook										4						
26 other salmon										1/0						
27 shark																
28 dogfish										2						
29 mackerel								0/2		5/7						
30 hake								1/4		20/30	10/24		1	1	3/13	8/10
31 mesopelagics									2	3					2	
32 sablefish															T	
33 lingcod																
34 skates & rays										2	2/1					
35 benthic fish-small										1	1					
36 rockfish-piscivore								1		3	7		1		8	25
37 rockfish-shelf plank.										2/1	T				2/1	2/1
38 rockfish-slope plank.										1/T	T				T/0	1/T
39 flatfish-benthic															T/0	
40 flatfish-water-column										5/7	6				3/4	8
41 flatfish-small										4/6	3				1/2	1
42 alcid										4	6/4		T		2/1	10
50 euphausiid-eggs	1	1/T	1		1	1						T				
51 fish-eggs		1/T	1	T								T		1		
52 pelagic detritus																
53 fishery offal															10	
54 benthic detritus															1	

TABLE 4 (continued)
Diet matrices for the spring and summer models. Values are wet weight percent (rounded to nearest whole percent) of each prey group (left column) in the diet of each predator group (top row). First value given is for the spring model, second value given is for the summer model when different, T = trace (<0.5%). Prey not shown are gulls, shearwaters, and mammals (groups 43–49) which have no predators in the models.

	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
1 phytoplankton																
2 copepods				53/21		1		17/11	2/5						56/27	
3 <i>E. pacifica</i>			3/10	4/12	2/24		1/2	1/3	T	T/1	3/5				2/18	
4 <i>T. spinifera</i>			3/20	4/30	2/24		1/2	1/3	T	1	3/5				3/17	
5 euphausiid-larvae															T	
6 pelagic amphipod			2/1	2	4/2		T	1							1/T	
7 macro-zooplankton			5/4	10	11/15		T	1		1	3/8				3	
8 small jellyfish			6	15	2											
9 large jellyfish			1	2	T						1					
10 pandalid shrimp	6/7	1/2	7/5	4/2	18/7	1	11/9	1								
11 benthic shrimp	20	4/6	6/3		15/5	2	10/9	6								
12 Dungeness crab	8	1	1			T	1	2								
13 epifauna	23	58/55	4/3		15/10	34	5	49		1		5	1/2			
14 infauna	3	30				63	T	12				2/4	1/2	98		
15 cephalopod	1	T	6/3	3	5		2/1	1	3/7	17/20	10/11	5	20/18	3	1	20/21
16 smelt			1	T	0/T		2/1	T	3/2	2/1	5/1	2/t	2			2/1
17 shad																
18 sardine	T/4		3/12	T/2	1		5/10	T/2	7/35	5/30	7/31	4/15	3/12		3/22	3/20
19 herring	4/1	1/0	27/7	2/T	15/1		25/4	3/1	71/30	49/20	58/20	29/6	23/4		28/6	32/6
20 anchovy																
21 juvenile salmon			0/T				T		1	T	0/T	T	T			T
22 juvenile rockfish			3/3	T	1		2	T	10	10	2/5	1/2	1/2		1/2	1/3
23 juvenile fish	6	2	5	T	1		3	T/1	1/7	3	5/10	2/5	2/4		2/5	2/5
24 coho										T		5/6	7/6		4	4
25 chinook							T			1		10/8	10/8		5/6	5/6
26 other salmon										T/0		1/0	2/0		1/0	1/0
27 shark																
28 dogfish													2/3			T/1
29 mackerel													2		5	5
30 hake	4/5		1/4	1			5/35					6/16	10/23		9/16	9/16
31 mesopelagics			5/2	1	1		1/T		1/2	2			2		5	5
32 sablefish							6/T						1		3	3
33 lingcod													1		T	T
34 skates & rays							1/T						1/2		T	T
35 benthic fish-small			4		2		4	3	T/1			5	2		2	2
36 rockfish-piscivore			T				1				3	1	3		2	2
37 rockfish-shelf plank.			T				1/T				T	1/T	1/T		T	T
38 rockfish-slope plank.																
39 flatfish-benthic	6		3				6	T				10/11	3/2		2/1	2/1
40 flatfish-water-column	1						2/1					1	1		2/T	2/T
41 flatfish-small	12/10	1	3	T		T	5	2		T		10	1/2		1	1
42 alcid																
50 euphausiid-eggs																
51 fish-eggs			1								1					
52 pelagic detritus																
53 fishery offal										8/10						
54 benthic detritus		2/3					1									

(*TL*), ecotrophic efficiency (*EE*), and biomass for groups that could not be determined empirically. Model-estimated biomasses were calculated using assumed ecotrophic efficiencies. In these cases, biomass accumulation rates were held at zero even though the model-derived biomass may differ between the spring and summer models.

Diet

Diet data for pelagic fishes (forage fish, salmon, sharks) came from observations made off the Oregon coast (Brodeur et al. 1987; Miller 2006). The diet data of the large jellyfish off the Oregon coast came from Suchman et al. (in press) and were converted from numerical fractions to weight fractions. The diets of demersal fishes, seabirds, and marine mammals came from the NCC food-web model of Field and Francis (2005). Diet matrices are presented in Table 4.

Fisheries

Quarterly commercial fisheries data were provided by the Pacific Coast Fisheries Information Network (PacFIN; <http://www.psmfc.org/pacfin/>). PacFIN landings data are organized north to south into five INPFC statistical regions as well as two broadly defined areas, the Oregon coast region and coast-wide landings for which no specific area has been recorded. The fraction landed in Oregon was estimated using a fractional area-overlap strategy. For non-salmon landings from unknown areas, 10% was assumed landed in Oregon and Washington and 63% of that was assumed landed in Oregon (by fraction of area within the 1,280 m isobath). For salmon landed from unknown areas, 90% was assumed landed north of California and 20% of that from Oregon in accord with the proportion of coho landings between Oregon and Washington in 2000 and 2002 (PFMC 2006a). The fraction of commercial landings inshore of the 125 m isobath was assumed based upon general trends apparent from the BPA and GLOBEC pelagic surveys, triennial groundfish survey, or best logical assumption: 100% inshore for smelt, shad, Dungeness crab; 75% inshore for shelf planktivore and piscivore rockfish, sardine, pandalid shrimp, infauna, epifauna; 25% inshore for shark, sablefish, miscellaneous small benthic fishes, lingcod, herring, flatfishes, dogfish, salmon, benthic shrimp; 10% inshore for skates and rays, mackerel, hake, cephalopods, anchovy; and 5% inshore for slope planktivorous rockfish.

Bi-monthly Oregon marine recreational landings data were acquired from the Pacific States Marine Recreational Fisheries Information Network (RecFIN; <http://www.psmfc.org/recfin/>). The fraction of recreational landings inshore of the 125 m isobath was estimated in the same manner as commercial landings.

Harvest rates used in the spring and summer models were the mean of the 2000 and 2002 rates. Discards were assumed to be 10% of landings.

Ecosystem Analysis

At the level of individual trophic groups, Ecopath calculates energy flow into and out of each group, accounting for all energy sources and destinations, and organizes this information as an energy consumption matrix. Ecopath also calculates ecotrophic efficiency (*EE*) or estimates the unknown biomass of a group as that required to support higher trophic levels given an assumed *EE*. Finally, each group's fractional Trophic Level (*TL*), or position in the food web relative to its distance from primary producers (or detritus), is calculated as $1 + (\text{the weighted average of the trophic levels of all prey organisms})$. By definition, $TL = 1$ for primary producers and detritus groups.

Ecosystem structure and status were analyzed in terms of energy flow and fate metrics: ecosystem size in terms of energy flow, energy flow between major sub-systems and trophic groups, source of consumed energy (primary production, detritus), and fate of consumed energy. The defined sub-systems are the primary producers, detritus, the pelagic sub-system (zooplankton, jellyfish, pelagic fishes, cephalopods, mesopelagic fishes, seabirds, and mammals), and the benthic sub-system (epifauna, infauna, demersal fishes). Energy flow metrics were calculated from the consumption matrix generated by Ecopath. The primary metric of overall ecosystem size is the Total System Throughput (TST), the sum of all energy flows within the ecosystem (Ulanowicz 1986).

Mixed Trophic Impact (MTI) analysis quantifies the total strength of direct and indirect linkages between every component of the ecosystem (Ulanowicz and Puccia 1990). The MTI matrix provides an index of the relative positive or negative impact that a small, hypothetical increase in the biomass of one trophic group would have upon every other group and can be considered a class of sensitivity analysis.

RESULTS

Balanced Models

A simplified version of the summer trophic network is illustrated in Figure 2. The simplified model is formed by aggregating similar trophic groups for illustrative purposes; subsequent analyses and discussion refer to the full models. Trophic groups are arranged along the y-axis by trophic level, box height is proportional to biomass, and the connecting lines are proportional to the log-scaled energy flow rate.

While the pelagic sub-system is almost exclusively supported by phytoplankton, most energy supporting the benthic sub-system is detrital in origin. Within the

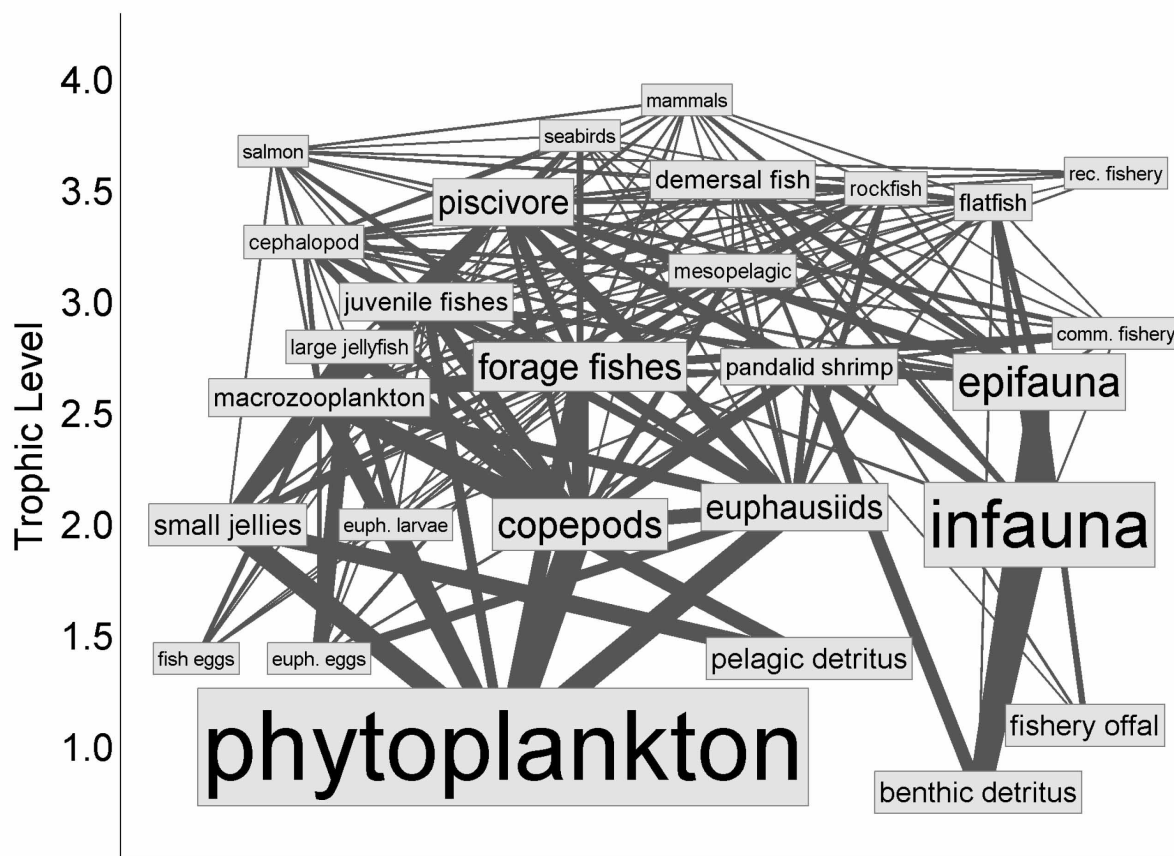


Figure 2. A simplified summer food-web model for the Oregon inner-shelf ecosystem. Box height is proportional to trophic group biomass, and box position along the y-axis marks the group's trophic level. Line width is proportional to the log of the energy flow rate. The pelagic system groups are to the left and are largely supported by phytoplankton production, the benthic system groups are to the right and are supported by detritus.

pelagic sub-system, jellyfish and forage fishes are at similar trophic levels (2.8–3.2). Seals, sea lions, and sharks occupy the highest trophic levels (>4.2) and have low *EEs*, indicating that little of the energy they consume is further used in the system. Within the benthic sub-system, lingcod and the water-column feeding flatfish (Pacific halibut, arrowtooth flounder, petrale sole) occupy high trophic levels (4.0–4.3) due to their fish-rich diet that includes piscivorous hake; however, unlike other high-*TL* groups, their high *EEs* show that much of their production is further used in the system.

Ecosystem Size

System-level metrics and indices for the spring and summer models are provided in Table 5. From spring to summer, the ecosystem doubles in size in terms of biomass (from 138 to 254 t/km², respectively) and nearly triples in size in terms of total energy flow (total system throughput, TST; 14,304 to 40,333 t/km²/yr) and in terms of total production (5,615 to 14,573 t/km²/yr).

The size of the living heterotrophic ecosystem, excluding primary production, the flow of material to detritus, and fisheries extraction, may be defined as the

TABLE 5
System-level metrics of the spring and summer food-web models for the Oregon inner-shelf ecosystem.

	SPRING	SUMMER	units
Total biomass (excluding detritus)	137.60	253.90	t/km ²
ENERGY FLOW METRICS			
Total net primary production	4857.97	13363.92	t/km ² /yr
Sum of all production	5615.47	14573.02	t/km ² /yr
Total System Throughput (TST)	14303.58	40332.53	t/km ² /yr
Sum of all consumption	3036.10	4838.78	t/km ² /yr
total pelagic sub-system consumption	2551.28	3976.56	t/km ² /yr
total benthic sub-system consumption	484.82	862.22	t/km ² /yr
Sum of all exports	2922.77	10483.31	t/km ² /yr
Sum of all respiratory flows	1671.87	2661.18	t/km ² /yr
Sum of all flows into detritus	6672.51	22348.91	t/km ² /yr
Flow INTO detritus (excluding flow between detritus pools)	3415.94	11295.35	t/km ² /yr
Flow FROM detritus (excluding flow between detritus pools)	438.46	765.24	t/km ² /yr
FISHERY STATUS INDICES			
Total catches	2.23	9.18	t/km ² /yr
Mean trophic level of the catch	3.19	2.88	
Gross efficiency (catch/net primary production)	0.000459	0.000687	

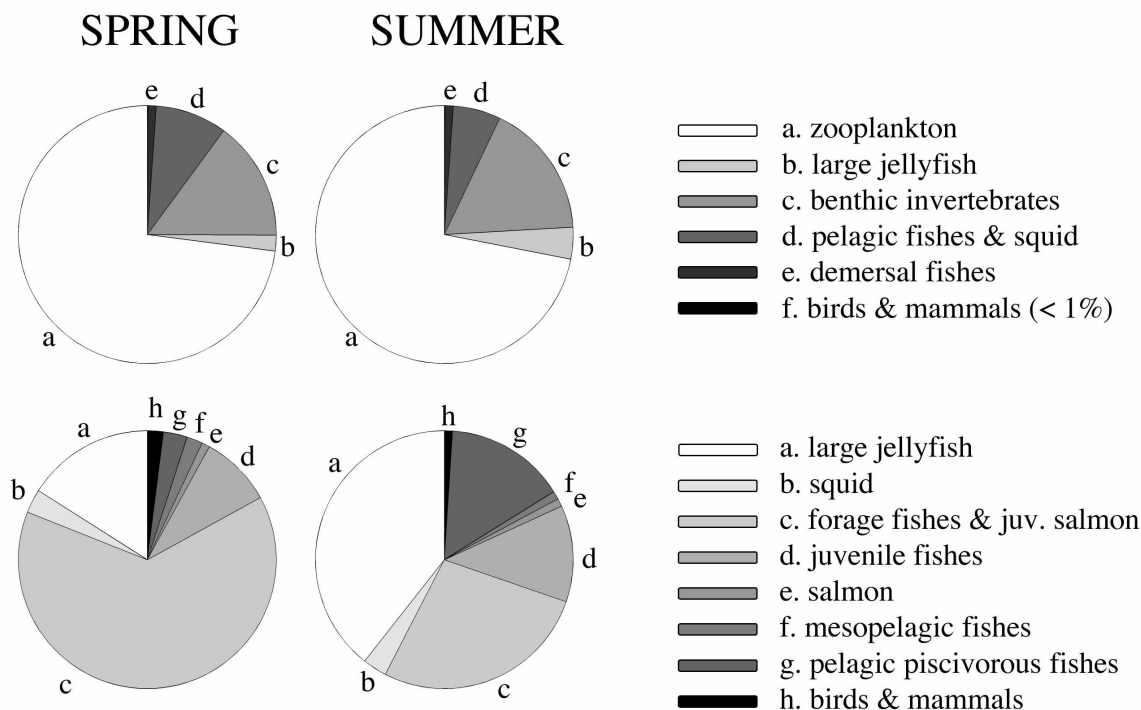


Figure 3. (Top) The relative sizes of the major trophic groups in terms of consumption rates within the spring and summer models: zooplankton (copepods, euphausiids, pelagic amphipods, macro-zooplankton, small jellies), pelagic fishes and squids (squid, forage fishes, juvenile fishes, salmon, piscivorous fishes, mesopelagic fishes), benthic invertebrates (pandalid shrimp, benthic shrimp, Dungeness crab, epifauna, infauna), benthic fishes (sablefish, lingcod, skates and rays, rockfishes, flatfishes). (Bottom) The relative sizes of groups within just the pelagic subsystem (excluding zooplankton) showing substantial changes from spring to summer in the relative sizes of the large jellyfish and forage fish groups.

total consumption by all trophic groups and grows by 60% from spring to summer (3,036 to 4,839 t/km²/yr). The living ecosystem is dominated by the zooplankton (copepods, euphausiids, pelagic amphipods, macro-zooplankton, and small jellyfish) and benthic invertebrates (pandalid and benthic shrimp, Dungeness crab, epifauna, and infauna) which account for 88% of the energy flow through the ecosystem in both spring and summer. Pelagic fishes and squids (6–9%), jellyfish (2–4%), demersal fishes (1%), and seabirds and mammals (<1%) account for the balance of the energy flow (fig. 3, top). The pelagic sub-system (zooplankton, jellyfish, pelagic fish and squid, birds and mammals) is five times larger than the benthic sub-system (benthic invertebrates, demersal fishes) in both seasons, though there are substantial seasonal changes in the pelagic sub-system within the trophic levels above zooplankton. In the spring, the dominant consumers are the forage fishes (64%) and the jellyfish (16%). In the summer, jellyfish (39%) become the dominant consumers followed by forage fishes (27%), pelagic piscivores (15%), and juvenile fishes (12%) (fig. 3, bottom). The total consumption among the higher trophic level groups in the spring and summer models is illustrated in Figure 4. Readily apparent is the increasing importance of the large jellyfish as the dominant consumer as the upwelling season progresses.

Predation upon Zooplankton

The relative importance of the different groups that prey upon the zooplankton community within the pelagic environment is presented in Figure 5. The importance of fish and jellyfish as predators upon different zooplankton groups appears to depend upon season as well as the size and swimming ability of the zooplankton prey. Jellyfish are the dominant consumers of euphausiid eggs and larvae and of small jellies in both seasonal models. Fishes remain the dominant consumers of adult euphausiids, macro-zooplankton, and pelagic amphipods in both seasons. As forage fishes become less abundant over the inner-shelf in the late summer, other pelagic fishes (e.g., juvenile fishes, hake, and mackerels) become the dominant consumer of these large-bodied zooplankton groups rather than the rapidly growing jellyfish population. For copepods and fish eggs, the relative importance of jellyfish as predators increases modestly as the overall abundance of the forage fishes declines.

Energy Flow Through the Ecosystem

The fate of energy consumed by a trophic group or sub-system is one of the following: to be passed on to higher trophic levels via predation, passed on to detritus through egestion or non-predation mortality, used for metabolism, stored as accumulated biomass, or

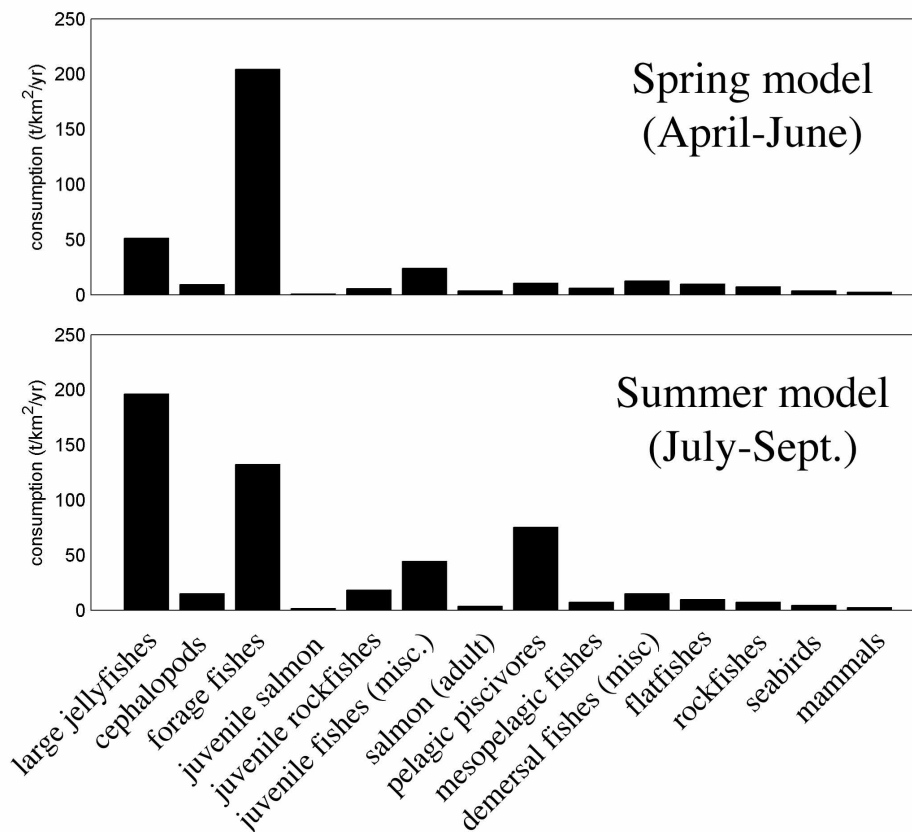


Figure 4. Consumption rates of upper trophic levels excluding plankton and benthic invertebrates (t/km²/yr). While the amount of energy flowing through the small pelagic forage fishes decreases from spring to summer, the amount flowing through the large jellyfish increases dramatically.

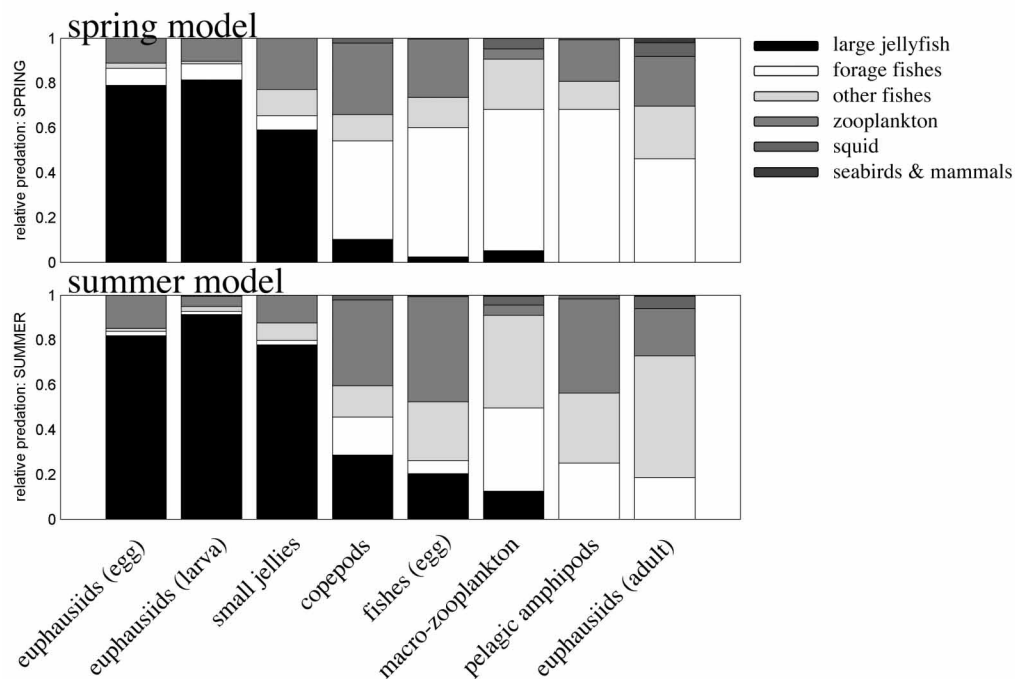


Figure 5. Relative predation upon zooplankton groups by upper trophic levels in the spring and summer food-web models. In the spring model, small pelagic forage fishes are an important consumer of lower trophic-level production; in the summer model, their importance is supplanted by large jellyfish and other pelagic fishes.

TABLE 6
Flow and fate of gross energy consumption (input) to unassimilated egestion, respiration, detritus (non-predation mortality), somatic growth, benthic predation, pelagic predation, or fishery harvest organized by major trophic aggregation or sub-system (t/km²/yr).

	input	output				to upper trophic levels		
		egestion	respiration	detritus	growth	benthic	pelagic	fishery
SPRING								
primary production	4858.0			2512.0	187.5	0.0	2158.5	0.0
pelagic environment (total)	2551.3	510.3	1401.7	281.7	36.3	15.7	304.4	1.2
zooplankton	2231.4	446.3	1222.6	246.5	23.3	8.5	284.1	0.0
large jellyfish	51.3	10.3	28.2	1.8	9.6	0.2	1.2	0.0
pelagic fish & squid (total)	263.0	52.6	146.4	33.4	3.4	7.0	19.1	1.2
squid	9.3	1.9	5.1	0.2	0.0	0.8	1.3	0.0
forage fish	204.6	40.9	112.5	31.8	3.4	4.3	11.2	0.4
juvenile fishes	29.5	5.9	16.2	0.7	0.0	1.2	5.5	0.0
salmon	3.5	0.7	2.3	0.3	0.0	0.0	0.2	0.0
pelagic piscivores	10.3	2.1	6.7	0.2	0.0	0.4	0.2	0.7
mesopelagic fishes	5.8	1.2	3.5	0.1	0.0	0.4	0.6	0.0
birds & mammals	5.7	1.1	4.5	0.0	0.0	0.0	0.0	0.0
benthic environment (total)	484.8	97.0	270.2	13.8	0.0	98.7	4.2	1.0
benthic invertebrates	455.7	91.1	250.6	13.2	0.0	96.1	3.8	0.7
demersal fish (total)	29.2	5.8	19.5	0.6	0.0	2.5	0.4	0.3
misc. demersal fishes	12.4	2.5	8.3	0.2	0.0	1.1	0.1	0.1
flatfishes	9.5	1.9	5.8	0.3	0.0	1.3	0.1	0.1
rockfishes	7.3	1.5	5.4	0.1	0.0	0.2	0.1	0.1
SUMMER								
primary production	13363.9			9894.9	187.5	0.0	3281.5	0.0
pelagic environment (total)	3976.6	795.3	2183.3	402.2	37.4	28.8	521.6	7.9
zooplankton	3478.0	695.6	1899.5	351.0	23.3	22.1	486.4	0.0
large jellyfish	196.2	39.2	107.9	35.1	9.6	0.3	4.1	0.0
pelagic fish & squid (total)	295.8	59.2	170.7	16.1	4.5	6.3	31.1	7.9
squid	14.9	3.0	8.2	0.4	0.0	0.6	2.8	0.0
forage fishes	133.4	26.7	73.4	6.8	3.5	2.5	14.3	6.3
juvenile fishes	62.2	12.4	34.2	1.6	0.0	1.6	12.4	0.0
salmon	3.3	0.7	2.1	0.3	0.0	0.0	0.2	0.1
pelagic piscivores	74.9	15.0	48.6	7.0	1.0	1.5	0.4	1.5
mesopelagic fishes	7.0	1.4	4.2	0.1	0.0	0.2	1.0	0.0
birds & mammals	6.6	1.3	5.3	0.0	0.0	0.0	0.0	0.0
benthic environment (total)	862.2	172.4	477.8	23.2	0.0	168.5	19.0	1.3
benthic invertebrates	830.8	166.2	456.9	22.6	0.0	166.1	18.0	0.9
demersal fish (total)	31.5	6.3	20.9	0.6	0.0	2.4	0.9	0.4
misc. demersal fishes	14.7	2.9	9.7	0.3	0.0	1.1	0.6	0.1
flatfishes	9.5	1.9	5.8	0.2	0.0	1.3	0.3	0.1
rockfishes	7.3	1.5	5.4	0.1	0.0	0.1	0.1	0.2

removed from the system via fishery extraction. The total flow and fate of the energy passing through the major ecosystem groups are summarized in Table 6 as a set of energy budgets. For every group, most consumed energy is used for respiration (55–80%), followed by the non-assimilated fraction (20%).

The relative fraction of energy lost to detritus or passed upwards to higher trophic levels varies from group to group. As top predators, seabirds and marine mammals are energetic dead-ends; less than 1% of the energy they consume is passed upwards. Jellyfish are also an energy-loss pathway even though they are not at a high trophic level ($TL = 2.8$); they are preyed upon by few other groups and only 2% of the energy consumed by jelly-

fish is passed on to higher trophic levels. In contrast, 10–15% of the energy consumed by pelagic fishes and cephalopods is transferred upwards. At the sub-system level, the benthic sub-system is more efficient than the pelagic sub-system, passing to higher trophic levels on average 21–22% of the energy consumed compared to 13–14% for the pelagic sub-system.

Seasonally, there is little change in the relative efficiency in which each group passes along consumed energy. The notable exception is the forage fishes. In the spring, only 8% of the energy consumed by forage fishes is transferred, whereas in the summer 17% is transferred. The low spring transfer efficiency may be attributed to export from the system via migration out of the model domain,

SPRING MODEL: mixed trophic impact

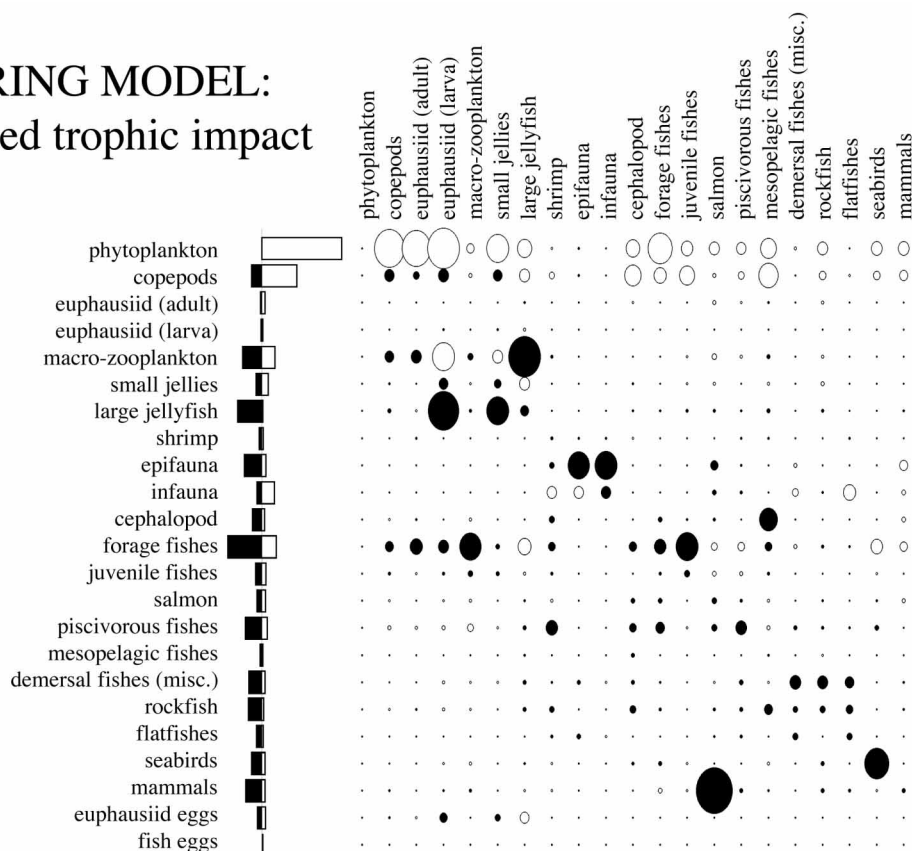


Figure 6. The Mixed Trophic Impact matrix (MTI) showing the relative impact, direct and indirect, that a small change in the biomass of a given trophic group will have throughout the spring food-web model. Rows down the side are the impacting groups and columns across the top are the impacted groups. White ovals represent positive impacts, black ovals represent negative impacts; oval size is proportional to impact strength. The bar chart represents the summed impact that each group has throughout the food web, positive or negative.

especially by herring. In the models developed here, the decline in forage fish biomass from spring to summer is assumed to be due to migration rather than predation.

Mixed Trophic Impact (MTI)

The mixed trophic impact matrices generated from the simplified spring and summer models (see above) are presented in Figures 6 and 7, respectively. The MTI matrices show the combined direct and indirect impacts that a hypothetical small increase in the biomass of one group will have on the biomass of every other group in the ecosystem. The impact units are dimensionless but allow the relative scale of impact across all groups in the ecosystem to be compared directly. An increase in phytoplankton biomass has a positive impact throughout the food web. The diagonal running from upper left to lower right shows that all groups, except phytoplankton, have negative impacts upon themselves.

Jellyfish exerted top-down influence upon zooplankton, especially upon euphausiid larvae and the small jellyfish. However, they had relatively little bottom-up impact upon higher trophic levels nor strong negative impact upon

forage fishes even in the summer months when jellyfish biomass (and potential competition for prey) was highest.

Forage fishes have a negative impact upon lower trophic levels, especially upon the macro-zooplankton. This top-down influence is greater in the summer. They have an indirect positive impact upon the large jellyfish that can be attributed to forage fish predation upon macro-zooplankton, which include species that consume jellyfish as a small part of their diet. Forage fishes have a positive, bottom-up impact upon salmon, seabirds, and mammals during the summer. Interestingly, the impact of forage fishes upon the piscivorous fishes changes from positive in the spring to weakly negative in the summer, perhaps because of the negative impact forage fish have upon euphausiids, which become a more important part of the piscivorous fish diet in the summer model.

The largest change in the ecosystem from spring to summer is related to the seasonal migration of pelagic piscivores (sharks, hake, mackerel) into the region. The negative impact that piscivorous fishes have upon squid, forage fish, salmon, and piscivorous fishes themselves increases from modest in the spring to strong in the sum-

SUMMER MODEL: mixed trophic impact

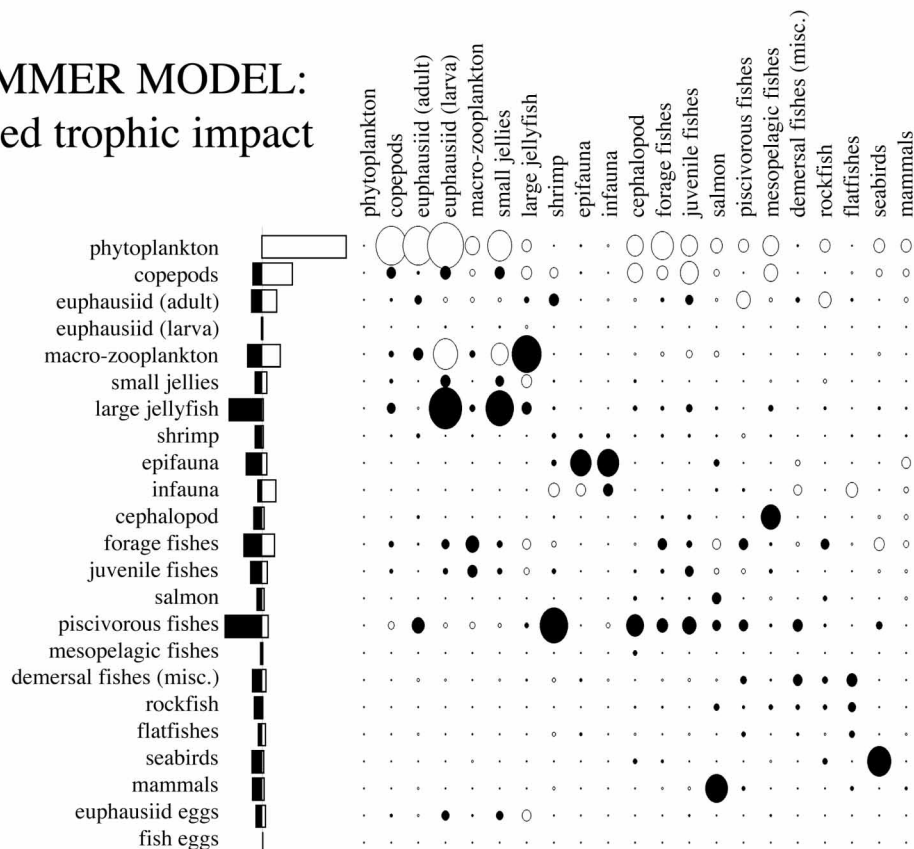


Figure 7. The Mixed Trophic Impact matrix (MTI) showing the relative impact, direct and indirect, that a small change in the biomass of a given trophic group will have throughout the spring food-web model. Rows down the side are the impact-ing groups and columns across the top are the impacted groups. White ovals represent positive impacts, black ovals represent negative impacts; oval size is proportional to impact strength. The bar chart represents the summed impact that each group has throughout the food web, positive or negative.

mer. Predation upon forage fish engenders an indirect positive impact by piscivorous fishes upon zooplankton in spring and summer. However, while piscivorous fishes have an indirect positive impact upon adult euphausiids in the spring, increased predation by piscivores upon adult euphausiids, particularly by hake, leads to a strong, direct negative impact in the summer model.

DISCUSSION

Importance of Jellyfish to the Ecosystem

Jellyfish are important predators in both high- and low-productivity ecosystems (Mills 1995). Most medusae are passive, generalist predators and show positive selection for fish eggs and larvae as these prey are relatively large (enhancing predator-prey encounter rates) and have little or no escape ability (Purcell and Arai 2001). Purcell and Grover (1990) have measured *Aequorea victoria* predation on larval herring within an embayment on Vancouver Island as over 50% of the standing stock per day. Off the Oregon coast, jellyfish predation impact upon fish recruitment has not been quantified, but observations off Oregon showed vir-

tually no fish eggs nor larvae in jellyfish diets (Suchman et al. in press), likely because of the scarcity of these potential prey compared to zooplankton rather than selection against fish eggs and larvae (C. Suchman, Virginia Institute of Marine Science, Gloucester Point, Virginia, pers. comm.). Also, fish larvae in this region are most abundant in early spring (Brodeur et al.²) before jellyfish biomass reaches high levels. However, consumption of larvae by younger stages of jellyfish than those examined by Suchman et al. (in press) could be occurring during the spring.

Generally, the predation impact upon copepods by jellyfish is too low to cause populations to decline (Purcell and Arai 2001; Purcell 2003). Other zooplankton groups can be more vulnerable, lacking the refuge of small size or the escape behavior of copepods (Suchman and Sullivan 2000; Hansson et al. 2005; Suchman et al. in press). In Prince William Sound, Alaska, jellyfish have been observed to consume up to 7% of the larvacean standing

²Brodeur, R. D., W. T. Peterson, T. D. Auth, H. L. Soulen, M. M. Parnel, and A. A. Emerson. Submitted-b. Abundance and diversity of ichthyoplankton as indicators of recent climate change in an upwelling area off Oregon. Mar. Ecol. Prog. Ser. NOAA/NMFS/NWFS, Newport, Oregon.

stock per day but only 0.3% per day of the copepod standing stock (Purcell 2003). Off Oregon, Suchman et al. (in press) observed that mean predation on the copepod standing stock by *Chrysaora fuscescens* was less than 1% per day but predation upon small jellyfish and euphausiid larvae was 10–12% per day. Jellyfish showed positive selection for euphausiid eggs and a grazing rate upon egg standing stock as high as 32% per day, suggesting that jellyfish have the potential to deplete euphausiid eggs over the inner-shelf (Suchman et al. in press). Adult euphausiids comprise a major share of the diet of many pelagic species in this system (Brodeur and Pearcy 1992; Miller 2006; Miller and Brodeur, 2007) and substantial consumption of their eggs by jellyfish could translate into reduced availability of adult euphausiids to pelagic predators.

Jellyfish predation on zooplankton may have more of an impact on ecosystem structure and energy flow than does predation on fish eggs and larvae. For example, *Aurelia aurita* is a top predator in the western Baltic Sea and in years of high abundance can initiate a trophic cascade that alters both zooplankton composition and phytoplankton abundance (Schneider and Behrends 1998). As they are preyed upon by few species, jellyfish could be a trophic dead-end. For example, Coll et al. (2006) found that in the Adriatic Sea, jellyfish is the major consumer in the pelagic sub-system and is an important trophic pathway, diverting production to the detritus and reducing the ecosystem-level transfer efficiency of energy to upper trophic levels. In our Oregon summer food-web model, when jellyfish biomass is at its peak, only 2% of the energy consumed by jellyfish was passed to higher trophic levels compared to 17% for forage fishes, or in absolute terms, while jellyfish consume almost 150% as much energy as the forage fish, they passed only 17% as much (calculated from values in tab. 6). Jellyfish have the potential to divert energy from the living ecosystem, increase the level of competition, and possibly reshape the trophic interactions within higher trophic levels.

This comparison supposes that the food value of jellyfish is comparable to other trophic groups. However, while the carbon content of copepods is roughly 9% of the wet weight (given dry : wet weight = 0.19 (Omori 1969) and C : dry weight = 0.45 (Uye 1982)), the carbon content of the jellyfish *Chrysaora fuscescens* is only 0.28% of the wet weight (Shenker 1985). Further, arthropods have more than five times the caloric value of jellyfish (Arai et al. 2003). The consequence is that if biomass were to be expressed in carbon or calories, the present models may overestimate the small fraction of jellyfish production returning to the living food web.

Besides energy density, food value is also a function of ease of digestion. The digestion rate of jellies (ctenophores) by chum salmon is more than 20 times that of pandalid shrimp; ctenophores and larger jellyfish

could be as important an energy source as other zooplankton despite their low energy content (Arai et al. 2003) if jellies were eaten at that much higher rate.

Could predation upon large jellyfish be higher than we estimate here? Gelatinous zooplankton are likely underrepresented in most diet studies due to their rapid digestion (Arai et al. 2003). However, almost all the studies to date that have shown that the fish that consume gelatinous zooplankton in any appreciable amount generally feed on smaller forms such as ctenophores, salps, and siphonophores, and few feed on the large medusae we consider here. A comprehensive study of the diets of 25 pelagic fish predators off the Oregon coast (Miller and Brodeur, 2007) found that gelatinous material never contributed more than 3% of the diet of any predator, and most of that contribution was from ctenophores. Dogfish may be important jellyfish predators (Arai 1988), but off the Oregon coast, gelatinous prey appear to make up less than 1% of their diet (Brodeur et al., in press). The majority of pelagic fish predators off the Oregon coast appear to be particulate feeders that consume whole prey (crustaceans, small fishes, small jellyfish). They lack the biting teeth to pull jellyfish apart. At the typical size of the sea nettle jellyfish (*Chrysaora fuscescens*) observed during surveys off the southern Oregon coast (>10 cm bell diameter, Suchman and Brodeur 2005), few of these are likely to be eaten whole by most fish or seabirds. Other species known to feed heavily upon large scyphozoa, ocean sunfish (Arai 1988), and sea turtles are present, but rare in Oregon waters. The carbon tied up in jellyfish, thus, is generally not available to the pelagic system, although it may provide a substantial nutrient input to the benthic food web when the medusae die and sink to the bottom of the ocean.

Do Jellyfish Compete with Planktivorous Fishes for Zooplankton Resources?

One hypothesis for the increasing jellyfish biomass within ecosystems worldwide is that overfishing of planktivorous fishes has reduced competition for zooplankton and opened niche-space which, by virtue of their rapid growth potential, jellyfish have been able to rapidly colonize (Mills 2001; Purcell and Arai 2001). As one example, overfishing of sardines and anchovies in the northern Benguela Current upwelling ecosystem may have led to their permanent replacement by jellyfish which now exceed the fish stocks in biomass (Lynam et al. 2006). There are few direct comparisons of jellyfish and forage fish diets (Purcell and Arai 2001). For example, Purcell and Sturdevant (2001) have observed a high degree of diet overlap between jellyfish and forage fishes in Prince William Sound, Alaska. Off Oregon, stable isotope analyses show that jellyfish are at a similar trophic level as forage fishes, while a comparison of the stomach contents

of jellyfish and many common forage fish shows a high similarity in their diets (Brodeur et al.¹). The food-web models we have developed incorporate these Oregon diet data in addition to growth and consumption rate estimates and show the extent of the potential for competition between jellyfish and forage fish.

The food-web models suggest that during the summer, jellyfish are responsible for eating more of the zooplankton production than are the forage fishes; jellyfish consume 17% of the total zooplankton production (excluding euphausiid and fish eggs) and forage fishes consume 9%. While in the spring, jellyfish consume 7% and forage fishes consume 22% of the zooplankton production. In terms of copepods alone, jellyfish consume 1.3% of the standing stock of copepods per day which amounts to 13% of the summer copepod production. This level of predation pressure is somewhat higher than Suchman et al.'s (in press) estimate that, off Oregon, *C. fuscescens* graze less than 1% of the copepod standing stock per day. This difference may be partly attributed to the model's aggregation of the four large jellyfish species.

While the models suggest that more zooplankton production flows through jellyfish than forage fishes, they do not show that competition for zooplankton prey actually occurs to a large enough degree as to cause the decline of forage fish stocks. Competition requires that zooplankton prey are limited by predation (Purcell and Arai 2001), and the models suggest that this was not the case in the early 2000s. A large proportion of the potential prey resource is not used by the living ecosystem; 44% of zooplankton production is lost to the detritus in the spring model and 40% is lost in the summer model. The MTI analysis (figs. 6 and 7) illustrates the modest impact that jellyfish have upon upper trophic levels. While jellyfish have a very strong negative impact on most zooplankton groups, they have very little impact on the upper trophic levels including the forage fishes.

Comparison to Other Upwelling Ecosystems

Trophic models have been developed for the four major eastern boundary upwelling ecosystems: the Benguela Current, the Humboldt Current, the California Current, and the Canary Current upwelling systems. From a set of inter-calibrated Ecopath models, the whole of the California Current system is shown to be the smallest of the four major upwelling ecosystems, an observation that may be partly attributed to the system's seasonality (Jarre-Teichmann et al. 1998). The seasonal models developed here for the northern California Current ecosystem off Oregon show that the total system throughput during the productive summer season is comparable to the annual mean size of the southern Benguela Current ecosystem and the Humboldt Current ecosystem off Peru, as estimated by Jarre-Teichmann et al. (1998).

Comparison of ecosystem structure among upwelling systems has revealed common traits: forage fishes dominate biomass and energy flow, there is generally low transfer efficiency of production to upper trophic levels, and upwelling systems are generally in a state of low maturity (Jarre-Teichmann et al. 1998). As in other upwelling systems, forage fishes are the major consumers in the spring model for the Oregon inner-shelf (fig. 4). However, by summer, jellyfish become the major consumer. A similar situation has occurred in the northern Benguela Current ecosystem in recent years where jellyfish consumption has become as great as that of the small planktivorous fishes (Moloney et al. 2005). One major difference between the northern California Current and the northern Benguela Current ecosystems, already stated, is the seasonality of the former. At present we can only speculate if this could moderate the impact that any future increase in jellyfish biomass could have off Oregon. Lynam et al. (2006) has hypothesized that the replacement of forage fishes by jellyfish in the northern Benguela ecosystem is irreversible due to the direct predation by jellyfish upon fish eggs and larvae, whereas the seasonal mismatch in jellyfish and ichthyoplankton abundance in the northern California Current ecosystem (Brodeur et al.¹) may offer some immunity from jellyfish predation.

Model Assumptions and Limitations

We have attempted to construct our seasonal models to incorporate the most complete and recent information available about the composition of the pelagic zooplankton and nekton community over the inner-shelf of Oregon based upon recent information from the BPA and GLOBEC pelagic surveys (Emmett et al. 2005) and the Newport Hydroline time-series data set (Keister and Peterson 2003). The efficiency of the rope-trawl used during the surveys is not known and catchability had to be assumed for each group. To the extent that independent estimates of biomass are available for the northern California Current (e.g., coast-wide stock assessment reports and acoustical surveys), they were used to inform our best guess of appropriate scaling factors to apply to catch-based biomass estimates. Attributing the change in community composition to local population growth (or mortality) or to migration was also a matter of making our best guess based upon what is known about the distribution and behavior of individual groups.

There are some particular processes and considerations that these models neglect and which could be incorporated in future model improvements. One of the most important of these processes is production export via Ekman transport during periods of strong upwelling. Surplus production that is lost to detritus in the current models may be more realistically assigned to export pro-

duction. Zooplankton production rate estimates used in these models, or any similar mass-balance food-web model for an upwelling ecosystem, may need to be increased to allow biomass advected offshore to be replaced. With respect to the seasonal change in biomass of some groups observed during ocean surveys, we assume the relative importance of immigration versus local growth and mortality as the cause. Resolving this issue for the most mobile groups will ultimately require incorporating real observations of growth rates and migration patterns during the model coverage years. In the absence of detailed information, we must rely upon more general observations or informed hypotheses of migration behavior. For groups in which empirical biomass data were unavailable and biomass was estimated by the model, we chose not to incorporate the hypothetical biomass accumulation rate when spring and summer estimates differed and avoided compounding our assumed biomass with assumed growth, mortality, and migration rates.

SUMMARY

The two seasonal food-web models developed here quantify direct and indirect trophic interactions with large jellyfish that are not amenable to direct observation. By summer, jellyfish become the major zooplankton consumer in the entire pelagic ecosystem, consuming nearly twice the zooplankton production as the pelagic forage fishes (anchovy, herring, sardine, smelt, and shad). In our model, jellyfish are an important pathway that diverts lower trophic level production away from upper trophic levels and reduces the efficiency of the entire ecosystem. Only 2% of the energy consumed by jellyfish is passed on to higher trophic levels while 10–15% of the energy consumed by forage fishes is transferred upwards. However, the impact of jellyfish upon the pelagic fish community as competitors may be moderate as more than a third of zooplankton production is not consumed at all but lost to the detritus. The strength of direct and indirect trophic linkages between large jellyfish and all other groups revealed by mixed-trophic impact analysis shows that jellyfish have a strong negative impact on most zooplankton but very little impact on upper trophic levels including forage fishes.

Food-web models provide a platform for testing the ramifications of our assumptions about physiological rates, diet, and migration, and for exploring ecosystem response to changes in any of these parameters, in community composition, or to other forcing phenomena. Future model development can and should address these questions: What if jellyfish, being easily digested and not easily quantified in diet studies, are consumed at a higher rate than supposed? At what level of jellyfish grazing does competition for zooplankton production limit the productivity and survival of small pelagic fish? Finally,

data on long-term changes in jellyfish biomass are very sparse and do not provide evidence of dramatic increases in the biomass off Oregon in recent years (Shenker 1984; Suchman and Brodeur 2005). However, given that jellyfish biomass has increased dramatically in other ecosystems around the globe, including upwelling ecosystems, modeling efforts to investigate the consequences of future jellyfish outbreaks to fisheries and throughout the food web are valuable.

Appendix: Data sources and parameters for trophic groups

The models developed here are based upon the northern California Current models developed by Field and colleagues (Field 2004; Field and Francis 2005; Field et al. 2006), but with expanded detail in the pelagic subsystem that incorporates recent pelagic survey data and is recast into a seasonal framework. Ecopath food-web models are typically developed to represent a full year, or several years. Physiological rate parameters are usually yearly averages. The models developed here are seasonal. They apply to the most productive half of the year, therefore production and consumption rate parameters are elevated above those used in other models. Seasonal models must also account for seasonal changes in biomass, expressed as biomass accumulation. Biomass accumulation, in turn, must be attributed to local production (or mortality), to immigration into the model domain (or emigration), or to a combination of both processes.

Phytoplankton: The phytoplankton group aggregates all taxa. Phytoplankton biomass is estimated from surface chlorophyll samples collected by the NH-line study (Peterson et al. 2002) assuming Chl *a* : N = 2.19 (Dickson and Wheeler 1995), C : N = 7.3 (Geider and La Roche 2002), wet weight : C = 10 (after Dalsgaard and Pauly 1997), and mixed layer depth = 26 m. Biomass accumulation from spring to summer is assumed to be due entirely to local production. $P/B = 180/\text{yr}$ based upon a doubling time of two days during the upwelling season.

Copepods: The copepod group is the aggregate of all copepod species present in the nearshore upwelling community and is dominated by boreal neritic species (*Pseudocalanus mimus*, *Calanus marshallae*, *Centropages abdominalis*, *Acartia longiremis*, *Acartia hudsonica*) (Peterson and Miller 1977; Keister and Peterson 2003; Morgan et al. 2003). Copepod biomass is estimated from the NH-line study; copepods were sampled with a 0.5 m ring-net towed vertically from near the sea floor (Peterson and Miller 1975; Keister and Peterson 2003; Peterson and Keister 2003). Copepod wet weight biomass is calculated from carbon biomass assuming C : dry weight = 0.45 and dry : wet weight = 0.19 (Omori 1969). Biomass accumulation from spring to summer is assumed

to be due entirely to local production. $P/B = 37/\text{yr}$ is based upon a growth rate of $0.1/\text{d}$ at 10°C (Hirst and Bunker 2003). Gross growth efficiencies (P/Q) for zooplankton groups generally range between 0.1 and 0.4 (Parsons et al. 1984). Consumption rates ($Q/B = 148/\text{yr}$) for copepods and other zooplankton groups were calculated assuming an intermediate growth efficiency, $P/Q = 0.25$.

Euphausiid juveniles and adults: The dominant euphausiid species off Oregon are *Euphausia pacifica* and *Thysanoessa spinifera* (Peterson et al. 2000). Each species is modeled individually since *T. spinifera* is a coastal species, and *E. pacifica* is most abundant over the outer shelf and shelf-break. *T. spinifera* is the only euphausiid common within the 150 m isobath off southwestern Vancouver Island (Mackas 1992). Off central Oregon, *T. spinifera* is in greatest abundance over the inner-shelf, and *E. pacifica* is in greatest abundance near the shelf-break (Smiles and Percy 1971; Peterson and Miller 1976).

Adult and juvenile euphausiid biomass is estimated from median monthly time-series density data collected at station NH-20 (128 m) from 2001 through 2004 (T. Shaw, OSU, Newport, Oregon, unpub. data). Vertical bongo tows from 20 m were conducted at night as euphausiids undergo diel vertical migration (Alton and Blackburn 1972), and vertically integrated concentrations are calculated assuming they are concentrated within the upper 20 m at night (W. T. Peterson, NOAA/NMFS, Newport, Oregon, unpub. data). Wet weights of juvenile and adult *E. pacifica* (6.31 mg, 66.51 mg) and *T. spinifera* (12.38 mg, 166.98 mg) are calculated from average juvenile and adult body lengths (*E. pacifica*, 7 mm and 18 mm, *T. spinifera*, 8 mm and 20 mm; T. Shaw, OSU, Newport, Oregon, unpub. data), applying an empirical length-carbon relation (Ross 1982), and assuming C : dry weight = 0.45 and dry : wet weight = 0.19 (Omori 1969).

Seasonal biomass accumulation in the model of *E. pacifica* is assumed to be entirely due to immigration via transport within bottom waters onto the inner-shelf during periods of upwelling (see Feinberg and Peterson 2003). Given that *T. spinifera* is a more coastal species, *T. spinifera* biomass accumulation is attributed to 20% local production and 80% immigration. $P/B = 5.8/\text{yr}$ for *E. pacifica* adults (Tanasichuk 1998a), and $P/B = 7.0/\text{yr}$ for *T. spinifera* (Tanasichuk 1998b) (excluding molt production). $Q/B = 23.2/\text{yr}$ for *E. pacifica* and $28.0/\text{yr}$ for *T. spinifera* (assuming growth efficiency, $P/Q = 0.25$).

Euphausiid larvae: Euphausiid larval biomass is estimated from the BPA zooplankton survey (see Methods), and seasonal biomass accumulation is assumed to be due entirely to local production. Areal biomass estimates assume larvae are concentrated within the sampled surface layer (30 m) (Lu et al. 2003; Lamb and Peterson

2005). $P/B = 69.8/\text{yr}$ is the mean of larval *E. pacifica* and *T. spinifera*, excluding molt production (Tanasichuk 1998a, b). $Q/B = 279.2/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$).

Euphausiid eggs: Euphausiid eggs are found off the central Oregon coast throughout the year, but the major spawning event occurs in late summer and has increased in the spring season following the northern Pacific climate regime shift in 1999 (Feinberg and Peterson 2003). After spawning, eggs hatch within two days at temperatures typical for the Oregon coast upwelling ecosystem (Feinberg et al. 2006). Estimates from the BPA zooplankton survey off northern Oregon in 2000 and 2002 suggest euphausiid egg biomasses of $0.2223 \text{ t}/\text{km}^2$ and $0.0010 \text{ t}/\text{km}^2$ in the spring and summer, respectively (tab. 2; C. Morgan, OSU, Newport, Oregon, unpub. data), and higher densities to the north off Washington. In our Oregon shelf models, we use estimates from central Oregon coast observations. Feinberg and Peterson (2003) report the mean spring euphausiid egg densities at NH-line stations NH-5 and NH-15 from 1999–2001 as $51.3/\text{m}^3$ and $11/\text{m}^3$, respectively, and summer densities as $132.6/\text{m}^3$ and $186/\text{m}^3$. Assuming that the negatively buoyant eggs (Gomez-Gutierrez et al. 2005) are distributed throughout the water-column, these mean areal densities of $2 \times 10^9/\text{km}^2$ in the spring and $1 \times 10^{10}/\text{km}^2$ in the summer provide the biomass estimates used in the models: $B_{\text{spring}} = 0.077 \text{ t}/\text{km}^2$ and $B_{\text{summer}} = 0.468 \text{ t}/\text{km}^2$. The assumed mean euphausiid egg wet weight (0.039 mg) is based upon the median *E. pacifica* and *T. spinifera* egg diameter of $415 \mu\text{m}$ (Gomez-Gutierrez et al. 2005) and a density of $1.039 \text{ g}/\text{cm}^3$ is from *Thysanoessa raschii* (Marschall 1983).

Within Ecopath, euphausiid eggs are handled as a non-feeding group in the same manner as a detritus group, following the example of Okey and Pauly for herring eggs (1999). Egg production rates are set as a detritus input rate parameter during model balancing to offset predation under an assumed ecotrophic efficiency of ≈ 0.9 .

Pelagic amphipods, macro-zooplankton, and small jellies: Pelagic amphipods include both hyperiid and gammarid amphipods in the planktonic community. Species most encountered during the BPA survey are *Themisto pacifica* and *Hyperia medusarum*. The macro-zooplankton group is an aggregation of meroplankton (crab zoeae and megalopae, barnacle larvae, mysid shrimp larvae, and echinoderm larvae), chaetognaths (e.g., *Sagitta* spp.), pteropods (e.g., *Limacina* spp., *Carinaria* spp., *Corolla spectabilis*, *Clione* spp.), ichthyoplankton, and pelagic polychaetes. The small jellyfish group includes salps, larvaceans, and ctenophores and has not been well sampled off Oregon (encountered during the BPA survey are *Cyclosalpa bakeri*, *Salpa fusiformis*, *Thetys vagina*, *Oikopleura*

spp., *Pleurobrachia* spp., *Beroe* spp.). Because of uncertain sampling efficiency and unknown biomass below the sampling depth of recent zooplankton surveys, seasonal biomass values of these groups are estimated by Ecopath under assumed ecotrophic efficiencies of 0.9. Model-derived biomass estimates (tab. 3) are substantially greater than estimates derived from the BPA zooplankton survey (tab. 2). For amphipods and macro-zooplankton, $P/B = 7/\text{yr}$ is from a British Columbia shelf model for carnivorous zooplankton (Preikshot 2005), and $Q/B = 28/\text{yr}$ is estimated under an assumed zooplankton growth efficiency ($P/Q = 0.25$). For the small jellyfish, $P/B = 9/\text{yr}$ and $Q/B = 30/\text{yr}$ is borrowed from the Fisheries Centre's (UBC, Vancouver, British Columbia) British Columbia shelf model for salps (Pauly and Christensen 1996).

Fish eggs: Fish egg biomass is obtained from the BPA zooplankton survey off northern Oregon assuming C : dry weight = 0.45 and dry : wet weight = 0.073 (as found for cod eggs, Thorsen et al. 1996) and eggs are concentrated within the surface 30 m. Within Ecopath, fish eggs are handled as a non-feeding, detritus-like group. Egg production rates are set as a detritus input-rate parameter during model balancing to offset predation under an assumed ecotrophic efficiency of ≈ 0.9 .

Large jellyfish: The large jellyfish group is an aggregate made up of the scyphomedusae *Chrysaora fuscescens* (sea nettles), *Aurelia labiata* (moon jellyfish), and *Phacellophora camtschatica* (egg yolk jellyfish), and the hydromedusa *Aequorea* spp. (water jelly). Abundance and biomass data is provided by the BPA and GLOBEC pelagic trawl surveys. Individual jellyfish wet weight and growth from spring to summer is provided by Suchman and Brodeur (2005). These size data were collected during the same GLOBEC cruises off southern Oregon as used in the present food-web models. Remotely Operated Vehicle observations over the Oregon shelf show that *Chrysaora fuscescens* extend throughout the water-column with peak abundance at or just below the depth sampled by the pelagic trawl survey (C. Suchman, Virginia Institute of Marine Science, Gloucester Point, Virginia, pers. comm.). To account for jellyfish below the trawl depth, biomass is conservatively scaled upward by a factor of 1.5. Being smaller in spring, jellyfish are sampled with less efficiency by the rope-trawl in spring than in the summer (Brodeur, NOAA/NMFS, Newport, Oregon, pers. obs.). The spring jellyfish biomass is further scaled upward relative to the summer biomass; the appropriate scaling factor is unknown but a factor of 3 implies a conservative estimate of productivity. Jellyfish biomasses used in the models are: $B_{\text{spring}} = 0.855 \text{ t*km}^2$, $B_{\text{summer}} = 3.269 \text{ t*km}^2$.

The unscaled change in biomass observed during the BPA and GLOBEC pelagic surveys over 0.25 yr from spring to summer (tab. 1) implies a production rate of $P/B = 12.3/\text{yr}$, assuming biomass accumulation to be

strictly endemic production and $B_{\text{mean}} = 0.643 \text{ t*km}^2$. Larson (1986) found the spring net jelly production rate in Saanich Inlet, Vancouver Island, to be 15/yr to 36/yr (ctenophores, hydromedusae, siphonophores). The re-scaled biomasses used in the present models imply lower productivity than measured by Larson or as calculated from the unscaled BPA and GLOBEC observations, but the latter are minimum productivity estimates that do not account for mortality and advection losses. Both the spring and summer models use $P/B = 15/\text{yr}$, which is at the low end of the range observed by Larson (1986). For our model, $Q/B = 60/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$).

Benthic invertebrates (pandalid shrimp, benthic shrimp, epifauna, crabs, infauna): The biomasses of pandalid shrimp, benthic shrimp, epifauna and infauna are estimated by Ecopath based on assumed ecotrophic efficiencies of 0.9. For pandalid shrimp (primarily *Pandalus jordani*) and benthic shrimp, $P/B = 3/\text{yr}$ are from natural mortality estimates for pandalid shrimp in Oregon (1.0–2.5/yr, and increased assuming higher productivity in spring and summer) (Hannah 1995), and $Q/B = 12/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$). Dungeness crab biomass is re-estimated from Field (2004); $P/B = 1/\text{yr}$ is increased from Field (2004) assuming higher productivity in spring and summer, and $Q/B = 4/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$). For epifauna and infauna: $P/B = 3/\text{yr}$ and is increased from Field (2004) assuming higher productivity in spring and summer, and $Q/B = 12/\text{yr}$ (assuming growth efficiency, $P/Q = 0.25$).

Forage fishes: The sampling efficiency of the trawl-system used in the BPA and GLOBEC pelagic surveys has not been tested for forage fishes (anchovy, smelt, herring, shad, sardines, and saury), and there are few independent estimates of forage fish biomass off Oregon against which to compare our biomass estimates. Nevertheless, these surveys remain unique in the NCC region for specifically targeting the pelagic fish community. During model balancing, we scale the total estimated forage fish biomass by a factor of 50, keeping the relative contribution of each forage fish group constant. Employing this scaling factor, the spring biomass in Oregon and Washington out to the 1,280 m isobath would be 382,000 t, or 7.5 t*km^2 (19.5 t*km^2 inshore, 1.2 t*km^2 offshore; BPA and GLOBEC survey data for offshore and Washington regions not shown). Preliminary estimates of the coastal pelagic species biomass as estimated from a coastwide acoustical survey in the spring of 2006 is approximately 2,000,000 t for the entire West Coast, most of which occurs south of Oregon (D. Demer, NOAA/NMFS, La Jolla, California, pers. comm.). Our forage fish biomass estimate would put 19% of the total West Coast biomass off Oregon and Washington. Simi-

larly, we estimate that the summer sardine biomass off Oregon and Washington would be 158,000 t, or 15% of the entire 2000 and 2002 West Coast sardine biomass of 1,057,000 t, as reported in the most recent stock assessment (Hill et al. 2006). Saury are largely offshore species and were encountered inshore in greater-than-trace numbers only in summer 2002 off southern Oregon; they are excluded from the inner-shelf models.

P/B ratios of 2/yr for smelt, shad, sardine, and anchovy are from the small pelagics group in the Fisheries Centre's (UBC, Vancouver, British Columbia) Strait of Georgia model (Pauly and Christensen 1996) and $P/B = 2.2/\text{yr}$ for herring is from their British Columbia shelf model. Q/B s are estimated under an assumed growth efficiency ($P/Q = 0.25$).

Salmon, adults and juveniles: For coho, Chinook, and "other" salmon (sockeye, chum, steelhead), a very crude estimate of the trawl-capture efficiency is calculated by comparing the summer coho biomass estimates from the pelagic surveys to the sum of the terminal run biomass (spawning returns plus freshwater landings) and ocean landings off Oregon and Washington (PFMC 2006b, 2007). These values (not shown) suggest a scaling factor of 3 to 6 between 2000 and 2002, and we use a scaling factor of 6. Juvenile salmon catchability is assumed to be the same as for adults and similarly scaled.

$P/B = 2.5/\text{yr}$, $Q/B = 16.5/\text{yr}$ for coho and $P/B = 1.9/\text{yr}$, $Q/B = 14.5/\text{yr}$ for other salmon (chum) are from Aydin et al. (2003). $P/B = 0.75/\text{yr}$ and $P/Q = 0.17$ for Chinook are from Great Lakes studies (Rand and Stewart 1998).

Mesopelagic fishes, squid, and non-salmonid juvenile fishes: Information about abundance and biomass of non-salmonid juvenile fishes ($< 5\text{cm}$), mesopelagic fishes, and squid from the BPA/GLOBEC pelagic surveys are considered non-quantitative due to capture efficiency limitations and net-avoidance. Biomasses are estimated by Ecopath under an assumed ecotrophic efficiency of 0.9.

$P/B = 3/\text{yr}$ for squid is borrowed from the Eastern Subarctic Pacific model of Aydin et al. (2003). $P/B = 2/\text{yr}$ for non-salmonid juvenile fishes is borrowed from the small pelagics group in the Strait of Georgia model (Pauly and Christensen 1996). Consumption rates for squid and juvenile fishes are calculated under assumed growth efficiencies ($P/Q = 0.25$). $P/B = 0.6/\text{yr}$ and $Q/B = 3/\text{yr}$ for mesopelagic fishes are modified from Field (2004).

Sharks: BPA and GLOBEC catch data are assumed to reflect regional biomass and are not adjusted for catchability. The species encountered during the pelagic surveys are the soupfin shark (*Galeorhinus galeus*), blue shark (*Prionace glauca*), common thresher shark (*Alopias vulpinus*), and salmon shark (*Lamna ditropis*). $P/B = 0.2/\text{yr}$ is from estimated natural mortality rates (PFMC 2003).

Hake and mackerels: The mackerels, jack mackerel

(*Trachurus symmetricus*) and Pacific mackerel (*Scomber japonicus*), are aggregated into a single group as in Field's (2004) NCC model. Hake (*Merluccius productus*) and mackerel biomasses from the BPA and GLOBEC pelagic surveys are considered underrepresented due to capture efficiency limitations and net avoidance during daylight trawls. Summer hake biomass is from the 2001 NOAA triennial bottom trawl survey and scaled by a factor of 1.25 to conservatively account for the pelagic population not sampled in the bottom trawl. The spring hake biomass is back-calculated based upon the relative rate of change observed during the BPA and GLOBEC surveys. Mackerel biomass is estimated from the BPA and GLOBEC pelagic surveys and scaled by a factor of 10. Both the hake and mackerel biomass densities are lower than used in Field's 1990s model but reflect the decline in piscivorous fish abundance observed during NOAA groundfish surveys in the late 1990s and during nighttime pelagic surveys off northern Oregon and southern Washington after 1998 (Field 2004; Emmett et al. 2006).

$P/B = 0.8/\text{yr}$ and $Q/B = 5/\text{yr}$ for hake are from the Fisheries Centre's (UBC, Vancouver, British Columbia) British Columbia shelf model (Pauly and Christensen 1996). $P/B = 0.5/\text{yr}$ for the mackerels is from estimates of Pacific mackerel natural mortality (Parrish and MacCall 1978), $Q/B = 7/\text{yr}$ is from Pauly and Christensen (1996).

Rockfishes: Rockfish are aggregated into three groups based upon general cross-shelf distribution and diet: shelf planktivores (stripetail, redstripe, greenstriped, canary, shortbelly, widow), shelf piscivores (bocaccio, chilipepper, cabezon, black, blue, China, quillback, black-and-yellow, gopher), and slope planktivores (darkblotched, splitnose, yellowmouth, sharpchin, Pacific ocean perch, aurora, blackgill, shortraker, rougheye). Biomasses are estimated from the 2001 NOAA groundfish survey with a 2X catchability adjustment for shelf piscivore and slope planktivore rockfish and a 6X catchability adjustment for shelf planktivore rockfish (assuming a higher density inshore of the 55 m isobath survey limit). Physiological parameters are modified from Field (2004).

Demersal fishes (dogfish, sablefish, lingcod, skates and rays, flatfishes, misc. small demersal fish): The defined demersal fish groups, their diets, and their physiological parameters are modified from Field (2004). The flatfishes are aggregated into three groups based upon diet: benthic feeders (English sole, Dover sole, rex sole), water-column feeders (Pacific halibut, arrowtooth flounder, petrale sole), and small flatfish (sanddabs, starry flounder, rock sole, slender sole, sand sole, butter sole). The miscellaneous small demersal fishes include sculpins, tomcod, eelpout, and snailfish, and their biomass is estimated by Ecopath based upon an assumed ecotrophic efficiency of 0.9. The biomass of all other demersal fish groups is estimated from the 2001 NOAA groundfish survey.

Seabirds and marine mammals: The dominant seabirds (alcsids, gulls, shearwaters) and marine mammals (harbor seals, sea lions, gray whales, baleen whales, toothed whales) parameters are modified slightly from Field (2004). Shearwaters are migratory and their relative spring and summer biomasses are adjusted to reflect this fact. The biomasses of other groups are adjusted to reflect the 125 m isobath offshore limits of the present models.

ACKNOWLEDGEMENTS

We thank the scientists and crews of the research and fishing vessels F/V *Frosti*, F/V *Sea Eagle*, R/V *W.E. Ricker*, and F/V *Ocean Harvester* for participating in the sampling at sea and the processing of samples in the laboratory. We thank Bill Peterson (NH-line data), Cheryl Morgan (BPA zooplankton data), Todd Miller (pelagic fish diet data), Tracy Shaw and Jennifer Menkel (euphausiid data), Cynthia Suchman (jellyfish diet data), Pete Lawson, Suzan Pool, Cindy Bucher, Bob Emmett, Susan Hinton, and Ben Wood (commercial fisheries data and queries). We also thank Ed Casillas, Hongsheng Bi, and two anonymous reviewers for their comments that improved the manuscript. Funding for the collection and analysis of the data comes from the NOAA Northwest Fisheries Science Centers, the NOAA Coastal Ocean Program as part of the U.S. GLOBEC program, and the Bonneville Power Administration. This is U.S. GLOBEC Program contribution number 558.

LITERATURE CITED

- Alton, M. S., and C. J. Blackburn. 1972. Diel changes in the vertical distribution of the euphausiids, *Thysanoessa spinifera* Holmes and *Euphausia pacifica* Hansen, in coastal waters of Washington. Calif. Fish Game 58:179–190.
- Arai, M. N. 1988. Interactions of fish and pelagic coelenterates. Can. J. Zool. 66:1913–1927.
- Arai, M. N., D. W. Welch, A. L. Dunsmuir, M. C. Jacobs, and A. R. Ladouceur. 2003. Digestion of pelagic Ctenophora and Cnidaria by fish. Can. J. Fish. Aquat. Sci. 60:825–829.
- Atrill, M. J., J. Wright, and M. Edwards. 2007. Climate-related increases in jellyfish frequency suggest a more gelatinous future for the North Sea. Limnol. Oceanogr. 52:480–485.
- Aydin, K. Y., G. A. McFarlane, J. R. King, and B. A. Megrey. 2003. The BASS/MODEL report on trophic models of the subarctic Pacific Basin ecosystems. North Pacific Marine Science Organization (PICES), Sydney, CA, PICES Scientific Report No. 25. 93 pp.
- Batchelder, H. P., J. A. Barth, M. P. Kosro, P. T. Strub, R. D. Brodeur, W. T. Peterson, C. T. Tynan, M. D. Ohman, L. W. Botsford, T. M. Powell, F. B. Schwing, D. G. Ainley, D. L. Mackas, B. M. Hickey, and S. R. Ramp. 2002. The GLOBEC Northeast Pacific California Current System Program. Oceanogr. 15:36–47.
- Brodeur, R. D., J. P. Fisher, R. L. Emmett, C. A. Morgan, and E. Casillas. 2005. Species composition and community structure of pelagic nekton off Oregon and Washington under variable oceanographic conditions. Mar. Ecol. Prog. Ser. 298:41–57.
- Brodeur, R. D., I. A. Fleming, J. M. Bennett, and M. A. Campbell. In press. Summer distribution and feeding of spiny dogfish (*Squalus acanthias*) off the Washington and Oregon coasts. In Management and biology of dogfish sharks. Am. Fish. Soc. Spec. Vol.
- Brodeur, R. D., H. V. Lorz, and W. G. Percy. 1987. Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979–1984. NOAA Technical Rept., NOAA-TM-NMFS-NWFS-57. 32 pp.
- Brodeur, R. D., and W. G. Percy. 1992. Effects of environmental variability on trophic interactions and food web structure in a pelagic upwelling ecosystem. Mar. Ecol. Prog. Ser. 84:101–119.
- Brodeur, R. D., H. Sugisaki, and G. L. J. Hunt. 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Mar. Ecol. Prog. Ser. 233:89–103.
- Christensen, V., and C. J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecol. Model. 172:109–139.
- Coll, M., A. Santojanni, I. Palomera, S. Tudela, and E. Arneri. 2006. An ecological model of the Northern and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts. J. Mar. Syst. doi:10.1016/j.jmarsys.2006.10.002.
- Dalsgaard, J., and D. Pauly. 1997. Preliminary mass-balance model of Prince William Sound, Alaska, for the pre-spill period, 1980–1989. Fisheries Centre Research Report 5. 34 pp.
- Dickson, M. L., and P. A. Wheeler. 1995. Nitrate uptake rates in a coastal upwelling regime: A comparison of PN-specific, absolute, and Chl *a*-specific rates. Limnol. Oceanogr. 40:533–543.
- Emmett, R. L., R. D. Brodeur, T. W. Miller, S. S. Pool, G. K. Krutzikowsky, P. J. Bentley, and J. McCrae. 2005. Pacific sardine (*Sardinops sagax*) abundance, distribution, and ecological relationships in the Pacific northwest. Rep. Calif. Coop. Ocean. Fish. Invest. 46:122–143.
- Emmett, R. L., G. K. Krutzikowsky, and P. Bentley. 2006. Abundance and distribution of pelagic piscivorous fishes in the Columbia River plume during spring/early summer 1998–2003: relationship to oceanographic conditions, forage fishes, and juvenile salmonids. Prog. Oceanogr. 68:1–26.
- Feinberg, L. R., and W. T. Peterson. 2003. Variability in duration and intensity of euphausiid spawning off central Oregon, 1996–2001. Progr. Oceanogr. 57:363–379.
- Feinberg, L. R., T. C. Shaw, and W. T. Peterson. 2006. Larval development of *Euphausia pacifica* in the laboratory: variability in developmental pathways. Mar. Ecol. Prog. Ser. 316:127–137.
- Field, J., and R. C. Francis. 2005. Mass balance models of the Northern California Current. UBC Fisheries Centre Research Reports, 13:207–216.
- Field, J. C. 2004. Application of ecosystem-based fishery management approaches in the Northern California Current. Ph.D. dissertation. University of Washington, Seattle. 408 pp.
- Field, J. C., R. C. Francis, and K. Y. Aydin. 2006. Top-down and bottom-up dynamics: linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. Progr. Oceanogr. 68:238–270.
- Geider, R. J., and J. La Roche. 2002. Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis. Eur. J. Phycol. 37:1–17.
- Gomez-Gutierrez, J., W. T. Peterson, and C. B. Miller. 2005. Cross-shelf life-stage segregation and community structure of the euphausiids off central Oregon (1970–1972). Deep Sea Res. II 52:289–315.
- Hannah, R. W. 1995. Variation in geographic stock area, catchability, and natural mortality of ocean shrimp (*Pandalus jordani*): some new evidence for a trophic interaction with Pacific hake (*Merluccius productus*). Can. J. Fish. Aquat. Sci. 52:1018–1029.
- Hansson, L. J., O. Moeslund, T. Kioerboe, and H. U. Riisgaard. 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). Mar. Ecol. Prog. Ser. 304:117–131.
- Hickey, B. M., and N. S. Banas. 2003. Oceanography of the U.S. Pacific Northwest coastal ocean and estuaries with application to coastal ecology. Estuaries 26:1010–1031.
- Hill, K. T., N. C. H. Lo, B. J. Macewicz, and R. Felix-Uraga. 2006. Assessment of the Pacific sardine (*Sardinops sagax caerulea*) population for U.S. management in 2006. NOAA Technical Rept., NOAA-TM-NMFS-SWFSC-386. 103 pp.
- Hirst, A. G., and A. J. Bunker. 2003. Growth of marine planktonic copepods: global rates and patterns in relation to chlorophyll *a*, temperature, and body weight. Limnol. Oceanogr. 48:1988–2010.
- Jarre-Teichmann, A., L. J. Shannon, C. L. Moloney, and P. A. Wickens. 1998. Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. S. Afr. J. Mar. Sci. 19:391–414.
- Kawahara, M., S. Uye, K. Ohtsu, and H. Iizumi. 2006. Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. Mar. Ecol. Prog. Ser. 307:161–173.
- Keister, J. E., and W. T. Peterson. 2003. Zonal and seasonal variations in zooplankton community structure off the central Oregon coast, 1998–2000. Progr. Oceanogr. 57:341–361.

- Lamb, J., and W. Peterson. 2005. Ecological zonation of zooplankton in the COAST study region off Central Oregon in June and August 2001 with consideration of retention mechanisms. *J. Geophys. Res. (C Oceans)*. 110:C10S15. doi:10.1029/2004JC002520.
- Larson, R. J. 1986. Seasonal changes in the standing stocks, growth rates, and production rates of gelatinous predators in Saanich Inlet, British Columbia. *Mar. Ecol. Prog. Ser.* 33:89–98.
- Lu, B., D. L. Mackas, and D. F. Moore. 2003. Cross-shore separation of adult and juvenile euphausiids in a shelf-break alongshore current. *Prog. Oceanogr.* 57:381–404.
- Lynam, C. P., M. J. Gibbons, B. E. Axelsen, C. A. J. Sparks, J. Coetzee, B. G. Heywood, and A. S. Brierley. 2006. Jellyfish overtake fish in a heavily fished ecosystem. *Cur. Biol.* 16:R492–R493.
- Mackas, D. L. 1992. Seasonal cycle of zooplankton off southwestern British Columbia: 1979–89. *Can. J. Fish. Aquat. Sci.* 49:903–921.
- Marschall, H. -P. 1983. Sinking speed, density and size of euphausiid eggs. *Meeresforsch.* 30:1–9.
- Miller, T. W. 2006. Trophic dynamics of marine nekton and zooplankton within the Northern California Current pelagic ecosystem. Ph.D. dissertation. Oregon State University, Corvallis, Oregon. 195 pp.
- Miller, T. W., and R. D. Brodeur. 2007. Diets of and trophic relationships among dominant marine nekton within the Northern California Current ecosystem. *U.S. Fish. Bull.* 105:548–559.
- Mills, C. E. 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems *ICES J. Mar. Sci.* 52:575–581.
- Mills, C. E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiol.* 451:55–68.
- Moloney, C. L., A. Jarre, H. Arancibia, Y. M. Bozec, S. Neira, J. P. Roux, and L. J. Shannon. 2005. Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. *ICES J. Mar. Sci.* 62:493–502.
- Morgan, C. A., W. T. Peterson, and R. L. Emmett. 2003. Onshore-offshore variations in copepod community structure off the Oregon coast during the summer upwelling season. *Mar. Ecol. Prog. Ser.* 249:223–236.
- Okey, T. A., and D. Pauly. 1999. Trophic mass-balance model of Alaska's Prince William Sound ecosystem, for the post spill period 1994–1996. *Fish. Cent. Res. Rep.* 7:135.
- Omori, M. 1969. Weight and chemical composition of some important oceanic zooplankton in the North Pacific. *Mar. Biol.* 3:4–10.
- Parrish, R. H., and A. D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. *Cal. Dept. Fish and Game Fish. Bull.* 167. 110 pp.
- Parsons, T. R., M. Takahashi, and B. Hargrave. 1984. *Biological Oceanographic Processes*, 3rd Edition. Pergamon Press, New York. 332 pp.
- Pauly, D., and V. Christensen. 1996. Mass-balance models of north-eastern Pacific ecosystems. *Fish. Cent. Res. Rep.* 4. 131 pp.
- Pennington, M. 1996. Estimating the mean and variance from highly skewed marine data. *Fish. Bull.* 94:498–505.
- Peterson, W. T., L. R. Feinberg, and J. E. Keister. 2000. Ecological zonation of euphausiids off central Oregon. *PICES Report* 15. http://www.pices.int/publications/scientific_reports/Report15/default.aspx.
- Peterson, W. T., and J. E. Keister. 2003. Interannual variability in copepod community composition at a coastal station in the northern California Current: a multivariate approach. *Deep Sea Res. II* 50:2499–2517.
- Peterson, W. T., J. E. Keister, and L. R. Feinberg. 2002. The effects of the 1997–99 El Niño/La Niña events on hydrography and zooplankton off the central Oregon coast. *Prog. Oceanogr.* 54:381–398.
- Peterson, W. T., and C. B. Miller. 1975. Year-to-year variations in the planktonology of the Oregon upwelling zone. *U.S. Fish. Bull.* 73:642–653.
- Peterson, W. T., and C. B. Miller. 1976. Zooplankton along the continental shelf off Newport, Oregon, 1969–1972. Oregon State University, Sea Grant College Program Publication No. ORESU-T-76-002. 111 pp.
- Peterson, W. T., and C. B. Miller. 1977. Seasonal cycle of zooplankton abundance and species composition along the central Oregon coast. *U.S. Fish. Bull.* 75:717–724.
- PFMC. 2003. Fishery management plan and environmental impact statement for U.S. West Coast Highly Migratory Species. Pacific Fishery Management Council, Portland, Oregon. http://www.pices.int/publications/scientific_reports/Report15/default.aspx.
- PFMC. 2006a. Review of 2005 Ocean Salmon Fisheries. Pacific Fisheries Management Council, Portland, Oregon. <http://www.pcouncil.org/salmon/salsafe05/salsafe05.html>.
- PFMC. 2006b. Preseason Report I: Stock Abundance Analysis for 2006 Ocean Salmon Fisheries. Pacific Fisheries Management Council, Portland, Oregon. <http://www.pcouncil.org/salmon/salsafe06/salsafe06.html>.
- Preikshot, D. 2005. Data sources and derivation of parameters for generalised Northeast Pacific Ocean Ecopath with Ecosim models. UBC Fisheries Centre Research Reports, 13:179–206.
- Purcell, J. E. 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.* 246:137–152.
- Purcell, J. E., and M. N. Arai. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiol.* 451:27–44.
- Purcell, J. E., and J. J. Grover. 1990. Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. *Mar. Ecol. Prog. Ser.* 59:55–61.
- Purcell, J. E., and M. V. Sturdevant. 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.* 210:67–83.
- Rand, P. S., and D. J. Stewart. 1998. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. *Can. J. Fish. Aquat. Sci.* 55:318–327.
- Ross, R. M. 1982. Energetics of *Euphausia pacifica*. I. Effects of body carbon and nitrogen and temperature on measured and predicted production. *Marine biology*, Heidelberg 68:1–13.
- Schabetsberger, R., C. A. Morgan, R. D. Brodeur, C. L. Potts, W. T. Peterson, and R. L. Emmett. 2003. Prey selectivity and diel feeding chronology of juvenile chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon in the Columbia River plume. *Fish. Oceanogr.* 12:523–540.
- Schneider, G., and G. Behrends. 1998. Top-down control in a neritic plankton system by *Aurelia aurita* medusae—a summary. *Ophelia*. 48:71–82.
- Shenker, J. M. 1984. Scyphomedusae in surface waters near the Oregon Coast, May–August, 1981. *Est. Coastal Shelf Sci.* 19:619–632.
- Shenker, J. M. 1985. Carbon content of the neritic scyphomedusa *Chrysaora fuscescens*. *J. Plankton Res.* 7:169–173.
- Smiles, M. C. J., and W. G. Pearcy. 1971. Size structure and growth rate of *Euphausia pacifica* off the Oregon coast. *U.S. Fish. Bull.* 69:79–86.
- Strub, P., J. S. Allen, A. Huyer, R. Smith, and R. Beardsley. 1987. Seasonal cycles of currents, temperatures, winds, and sea level over the Northeast Pacific continental shelf: 35°N to 48°N. *J. Geophys. Res.* 92:1507–1526.
- Suchman, C. L., and R. D. Brodeur. 2005. Abundance and distribution of large medusae in surface waters of the northern California Current. *Deep Sea Res. II* 52:51–72.
- Suchman, C. L., E. A. Daly, J. E. Kiester, W. T. Peterson, and R. D. Brodeur. In press. Feeding pattern and predation potential of scyphomedusae in a highly productive upwelling region. *Mar. Ecol. Prog. Ser.*
- Suchman, C. L., and B. K. Sullivan. 2000. Effect of prey size on vulnerability of copepods to predation by the scyphomedusae *Aurelia aurita* and *Cyanea* sp. *J. Plankton Res.* 22:2289–2306.
- Tanasichuk, R. W. 1998a. Interannual variations in the population biology and productivity of *Euphausia pacifica* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. *Mar. Ecol. Prog. Ser.* 173:163–180.
- Tanasichuk, R. W. 1998b. Interannual variations in the population biology and productivity of *Thysanoessa spinifera* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years. *Mar. Ecol. Prog. Ser.* 173:181–195.
- Thorsen, A., O. S. Kjesbu, H. J. Fyhnrd, and P. Solemdal. 1996. Physiological mechanisms of buoyancy in eggs from brackish water cod. *J. Fish Biol.* 48:457–477.
- Ulanowicz, R. E. 1986. *Growth and development: ecosystem phenomenology*. Springer Verlag, New York. 203 pp.
- Ulanowicz, R. E., and C. J. Puccia. 1990. Mixed trophic impacts in ecosystems. *Coenoses* 5:7–16.
- Uye, S. 1982. Length-weight relationships of important zooplankton from the inland Sea of Japan. *J. Oceanogr. Soc. Japan* 38:149–158.
- Weinberg, K. L., M. E. Wilkins, F. R. Shaw, and M. Zimmermann. 2002. The 2001 Pacific west coast bottom trawl survey of groundfish resources: Estimates of distribution, abundance, and length and age composition. NOAA Tech. Memo. NOAA-TM-NMFS-AFSC-128, 140 pp.