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Bottom-Up Ecosystem Trophic Dynamics Determine Fish Production in the Northeast Pacific

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The question of "bottom-up" versus "top-down" control of marine ecosystem trophic interactions was addressed using annual fish catch data and satellite-derived (SeaWiFS) chlorophyll-*a* measurements for the continental margin of western North America. Findings reveal a marked alongshore variation in retained primary production that is highly correlated with the alongshore variation in resident fish yield. Highest productivity occurs off the coasts of Washington and southern British Columbia. Zooplankton data for coastal British Columbia confirm strong bottom-up trophic linkages between phytoplankon, zooplankton, and resident fish, extending to regional areas as small as 10^4 km^2.

It remains unclear whether long-term sustainable fish catches from continental margin ecosystems are controlled largely by the primary production rate ("bottom-up" processes) or by predatory-prey interactions at higher trophic levels ("top-down" processes), including the fishery. Comparative cross-system analyses (*1*) suggest that bottom-up control is the principal mechanism. However, other studies, primarily of lake ecosystems, where it is easier to experimentally manipulate fish production, have found that top-down processes may prevail (*2*). While it is certain that at some high harvest level the fishery will begin to exert a controlling influence on fish production, the rate of removal at which this level occurs is uncertain. Here, we use satellite-derived estimates of mean annual chlorophyll-a concentration to test the hypothesis that long-term average fish production and yield within large-scale fishing zones along the continental margin of western North America are mainly controlled by phytoplankton production.

Satellite observations of surface chlorophyll-*a* (chl-*a*) concentration (Fig. 1)—a proxy measure of the surface phytoplankton concentration (*3*)—are available at a spatial resolution of 1.1 km from the water-leaving radiance (reflectance) measurements provided by the standard Seaviewing Wide Field-of-view Sensor (SeaWiFS) (*4*). The surface concentration of chl-*a* is also directly related to the rate of primary production (*5*). For the largest spatial scale examined in this study (average surface area 67,157 km^2), we calculated the mean annual chl-*a* concentrations for the years 1998 to 2003 for the eleven North Pacific Anadromous Fish Commission (NPAFC) statistical fishing areas (*6*). The NPAFC areas span the continental margin from southern California to western Alaska (Table 1; Fig. 1). Smaller-scale (average area 18,830 km^2) mean concentrations also were calculated for six oceanographically distinct fishing areas in western British Columbia (BC) (Fig. 1) identified by (*7*). Extensive zooplankton time series for BC (*8*) further make it possible to examine small-scale regional-scale trophic coupling between phytoplankton and zooplankton, and zooplankton and fish.

The mean chl-*a* values used in this study are those for which the Negative Water Leaving Radiance (NWLR) filter (*9*) has not been applied (NWLR-Off). For the regions we are studying, the correlation between the "filter-on" and "filter-off" versions of the mean annual chl-*a* data (Table 1) is near unity (*10*) so we arrive at the same conclusions regardless of which data set is compared with the fish catch data. The mean annual yields (catch in tonnes·km^{-2}) of "resident" and "highly migratory" fish species for the northeast Pacific continental margin have been calculated from long-term landing statistics compiled by the INPFC/NPAFC for the period 1960 to 1998. For the six BC fishing regions, long-term fish catch data are available for the period 1960 to 1991 (*11*). Resident species, such as herring and groundfish, are defined as those populations which occupy the continental margin year-round and undertake only spatially limited seasonal migrations. In contrast, highly migratory species are present in some fishing regions for only a short time each year. For example, sockeye, pink, and chum salmon undertake extensive northward migrations as juveniles along the continental margins of British Columbia and Alaska, before entering the Gulf of Alaska. These species return several years later as adults to spawn in their natal rivers. In the southern NPAFC regions, components of the Pacific hake, sardine and mackerel populations migrate northward from southern California in the spring as far as British Columbia, where they spend the summer foraging. These species migrate back to southern California in the fall, to spawn.

Large-scale trophic coupling. Table 1A presents the mean annual satellite-derived estimates of chl-*a* for the NWLR-Off (and, for comparison, the NWLR-On) data, together with the corresponding fish yields for the eleven large-scale NPAFC statistical areas spanning western North America. Bi-weekly chl-*a* concentrations are most variable in the Shumagin and Eureka regions and least variable in the Monterey and Conception regions (Table 1). There is a highly significant linear correlation (Fig. 2) between the long-term average resident fish yield (*LTY*; tonnes$\cdot$km^{-2}) and the mean annual chl-*a* concentration (mg$\cdot$m^{-3}), such that $LTY = 0.436 \times chl\text{-}a(\text{NWLR-off}) - 0.38$, with adjusted $r^2 = 0.87$. Thus, spatial variability in the annual chl-*a* concentration accounts for 87% of the spatial variance in the long-term yield of resident fish. These findings, combined with the observation that primary production is a function of the surface chl-*a* concentration, confirm a strong linkage between large-scale, area-specific rates of phytoplankton production and fish yield in the northeast Pacific.

From both an oceanographic and biological perspective, the NPAFC region can be divided into a Coastal Upwelling Domain, which spans NPAFC areas from Conception to Vancouver, and a Coastal Downwelling Domain, which spans the areas from Charlotte to Shumagin (*12*). An analysis of covariance of the resident fish yield and chl-*a* reveals that neither the type of domain, nor the domain-chlorophyll interaction effects, are significant. As a consequence, the relationship between fish yield and chl-*a* concentration in both domains is explained by a common intercept and slope.

Within the Coastal Upwelling Domain, annual offshore (seaward) Ekman transport associated with the upwelling-favorable alongshore winds that prevail over the continental margin (*13*), is highest in the south and diminishes with latitude, reaching near-zero values at the northern limit of the Upwelling Domain near 50° N (Fig. 3). Coincidently, there is a significant poleward increase in the average surface chl-*a* concentration, with the chl-*a* concentration at the spatial scale of the NPAFC regions negatively correlated ($p = 0.011$) with the annual cumulative seaward Ekman transport. The negative sign of this correlation is counterintuitive, evidence that factors other than wind-induced upwelling also are important for plankton productivity. For example, during spring to fall in the southern NPAFC regions, upwelling is frequently punctuated by flow events (*14*), which cause the seaward transport of plankton from the narrow (10-km scale) shelf to the deep ocean. As a consequence, a significant fraction of the primary production in the coastal region from Pt. Conception to 43°N becomes unavailable to the resident fish ecosystem.

Factors other than seaward export also contribute to the alongshore variation in primary productivity. In particular, the northward increase in coastal runoff from major rivers in the northeast Pacific leads to increased stability and shoaling of the upper layer, as well as an increase in the supply of land-derived nutrients. Accordingly, the highest annual average chl concentrations occur in the Washington-southern BC region where there is moderate upwelling and the first appearance of year-round freshwater flux (from the Columbia and Fraser rivers). The latter provides both stability and micro-nutrients. The continental margin off the BC-Washington coast is also wider than that off Oregon-California, so that more of the primary production remains on the shelf (*15*), where it is cycled through the pelagic and benthic food webs to the resident fish community.

In the Coastal Downwelling Domain from northern British Columbia to western Alaska, the large volume of freshwater entering the coastal ocean from major rivers continues to be a major source of micro-nutrients and upper ocean stability (*16*, *17*). Macro-nutrients are supplied through current-induced upwelling, coastal eddies and winter upwelling winds. Thus, chl concentrations remain moderately high despite the absence of summer upwelling.

Pacific hake is currently the most abundant migratory pelagic fish species in the northeast Pacific. As indicated in Table 1, the largest hake catches occur between 42 and 50° N, which is also the region of highest *chl-a* concentrations (Fig. 3). Components of the hake population are clearly migrating northward each spring from southern California to the most productive areas along the continental margin, where, in summer, they feed primarily on euphausiids and small forage fish, such as herring (*18*). As with resident fish stocks, the alongshore biomass of highly migratory fish stocks is strongly linked to primary productivity. However, because of the way the fishery is conducted, the area-specific catch of hake is not proportional to the amount of food hake consumed in each area during their annual migration. Consequently, there is more scatter in the linear regression linking migratory fish yields to chl-*a* concentration (Table 1).

Regional-scale trophic linkages. To determine if the significant correlation found for the NPAFC fishing areas holds at smaller spatial scales, we calculated the annual mean concentrations of chl-*a* and resident fish yield for the six BC coastal fishing areas. Between 1998 and 2003, the period for which annual SeaWiFS records are available, the highest mean annual chl-*a* concentration occurred in the Strait of Georgia (site BCF3), while the lowest concentrations were in areas BCF4 and BCF6 off the outer northwest coast (Fig. 1; Table 1). Bi-weekly chl-*a* concentrations are least variable in the Strait of Georgia (site BCF3) and most variable off the west coast of Vancouver Island (sites BCF1, BCF4 and BCF2; Table 1).

As with the NPAFC regions, the smaller scale BC regions show a significant linear correlation between the mean annual chl-*a* concentration ($mg \cdot m^{-3}$) and the mean annual resident fish yield ($tonnes \cdot km^{-2}$), with $LTY = 0.437 \times chl\text{-}a$(NWLR-off) + 0.08, with adjusted $r^2 = 0.76$, $p = 0.015$ (Table 1B). Based on an analysis of covariance for the British Columbia areas, the mean resident fish yield versus chl-*a* regression has the same slope as the LTY-chl regression for the large-scale NPAFC areas (Fig. 2).

Zooplankton abundance time series for coastal British Columbia have enabled us to extend our analysis to the regional-scale coupling between primary productivity (Fig. 4a) and secondary (zooplankton) productivity (Fig. 4b; *19*). Consistent with bottom-up trophic control, the mean annual zooplankton and chl-*a* concentrations for the six BC regions are highly correlated through the power-law function $Zoo = 46.57 \times (chl\text{-}a)^{0.488}$, with adjusted $r^2 = 0.85$; here, *Zoo* denotes zooplankton concentration ($mg \cdot [dry \cdot wt] \cdot m^{-3}$) and the mean chlorophyll concentration (NWLR filter-Off) is in $mg \cdot m^{-3}$. Presumably, this relationship is non-linear because zooplankton are unable to graze the larger concentrations of phytoplankton produced in the more fertile areas with the same trophic efficiency. In productive continental shelf regions, an increasing proportion of the phytoplankton biomass settles to the seafloor, and is ultimately transferred to the shelf fish community via the benthic food web. The relationship between resident fish yield and zooplankton in BC is linear (Fig. 4B): $LTY = 0.055 \times Zoo - 1.98$, with adjusted $r^2 = 0.79$ ($n = 6$, $p = 0.01$). Small zooplankton are an important food source for the early life history stages of all resident fish species, while larger zooplankton are an important food for many juvenile and adult resident fish.

Our analysis leads to several fundamental conclusions concerning marine food web interactions along the west coast of North America. Within the large-scale (67×10^3 km^2) NPFAC fishing areas extending from southern California to western Alaska, a large proportion (87%) of the spatial variation in long-term averaged resident fish production is controlled by "bottom-up" trophic interactions. On average, high regional primary productivity (represented by SeaWiFS chl-*a* data) produces high fishery yields. Plankton and fisheries data for coastal British Columbia further reveal that this linkage extends to much smaller spatial scales (19×10^3 km^2) than previously considered. Regression of the long-term average resident fish yield against chl-*a* concentration yields the same regressional slope for both the Coastal Upwelling and Coastal Downwelling domains, a highly unexpected result because the biological diversities of the zooplankton, and migratory and resident fish communities in these domains are quite distinct. The similar regressional slopes for both the intense upwelling and intense downwelling regions demonstrates that the available primary production is channeled through the pelagic and benthic food webs to the resident fish community with approximately the same conversion efficiency in each domain. We further find that the resident fish yields in summer upwelling regions increase poleward, in inverse proportion to the annual accumulative seaward Ekman transport over the continental margin, reaching a maximum in southern British Columbia near the northern limit (50° N) of the Coastal Upwelling Domain. The highly productive areas of southern British Columbia and northern Washington—corresponding to the transition region between the low annual coastal runoff of California to the high coastal discharge of Alaska—are also near the northern foraging limit of the migratory Pacific hake and sardine populations in the northeast Pacific. Resident fish yields continue to remain relatively high northward along the Alaska coast despite the absence of significant coastal upwelling. Consequently, the tightly coupled phytoplankton-fish relationship we observe for the west coast of North America must be maintained by an onshore nutrient supply, late-winter "preconditioning" of the surface ocean (*20*), and (or) upper ocean stability associated with freshwater discharge from major rivers along the coast.

The resident fish catch time series for the Conception to Columbia regions indicate that the fish yields increased in the 1960s and 1970s, peaked in the early 1980s, and have since declined. A climatic regime shift, characterized by warmer upper ocean temperatures, occurred in the northeast Pacific in 1976. About the same time, zooplankton concentrations started to decline off southern California (*21*). These observations suggest that, in addition to harvesting, a coincident decline in zooplankton biomass (and production) may have contributed to the recent downward trend in fish yield in this region. This possibility is in broad agreement with (*22*), who found that an increase in water temperatures in warmer regions in the Northeast Atlantic lead to a decrease in phytoplankton abundance.

References and Notes

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2. M. Scheffer, S. Rinaldi, and Y.A. Kuznetsov. *Can. J. Fish. Aquat. Sci.* **57**, 1208 (2000).
3. Satellite-based phytoplankton pigment (chlorophyll-*a*) estimates are derived from water-leaving radiance at near-infrared frequency bands following correction for atmospheric optical properties (S. Tassan, *Applied Optics* 33, 2369 (1994)). Except for highly turbid coastal waters, where the optical properties of inorganic suspended matter and colored dissolved organic matter can be problematic (K.G. Ruddick, F. Ovidio, M. Rijkeboer, *Applied Optics*

39, 897 (2000)), the calibrated radiance data are a proxy for surface phytoplankton concentration.

4. Chlorophyll-*a* concentrations are derived from the ratio of radiance at the 510 and 555 nm frequency bands by the SeaWiFS sensor aboard the SeaStar spacecraft launched in August 1997.
5. In the Columbia region, the depth-integrated daily rate of primary production is linearly correlated with the surface chl-*a* concentration (M.J. Perry, J.P. Bolger and D.C. English. In *Coastal Oceanography of Washington and Oregon,* M.R. Landry and B.M. Hickey (Eds.). Elsevier. Amsterdam (1989)).
6. Long-term average fish catches were compiled from data summarized in the INPFC/NPAFC statistical yearbooks for the period 1960-1998 [Available from NPAFC Secretariat, Suite 502, 889 W. Pender St., Vancouver, BC, V6C 3B2, Canada] by M.V.H. Lynde, *NOAA Technical Memo., NMFS/NWC-103* (1986), and in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) report series. The catch time series indicated that the fisheries were well developed by 1960 in every area, except Yakutat, Chirikof and Shumagin, which had developed by 1966, and Columbia and Kodiak by 1975. Long-term mean catches were estimated for each area for the period starting with the aforementioned years to 1998 (the most recent data available). For each region the catch was partitioned into "resident" species and "highly migratory" species. Resident species (of which there are >20 interacting species in the northeast Pacific) inhabit the continental margin and undergo limited along-shelf and cross-shelf seasonal movements. In contrast, in the five southern NPAFC areas, Pacific hake, sardine and the mackerels undergo extensive annual north-south migrations. Accordingly, these species, plus the mobile anchovy populations were classified as "highly migratory". In the five northern NPAFC areas (Shumagin to Charlotte) the entire catch consisted of "resident" species, primarily groundfish and herring. In the five southern areas, the resident fish community also includes herring and groundfish (but not hake). However, in this region a significant fraction of the total catch consisted of highly migratory species (Table 1A). Regional "resident" and "highly migratory" fish yields were estimated by dividing the respective catches by the surface area of each region.
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8. Monthly mean estimates of total zooplankton concentrations (mg·[dry weight]·m^{-3}) were derived for the six coastal regions in BC. The data (mostly collected between 1992 and 2002) were obtained from the Institute of Ocean Sciences, Sidney, BC [available from Steve Romaine]. The raw data were sorted into the respective coastal region where the samples were collected. The original 53 zooplankton species groups were reduced to 8 functional groups. An ANOVA indicated a highly significant night-day sampling effect for euphausiids. Euphausiid night biomasses were 2.8 to 5.4 times higher than the day biomasses. The night/day ratio was species-specific. Accordingly, euphausiid samples collected during the day were corrected by multiplying the day biomass by the species-specific night/day correction factor. There was no significant day-night sampling effect on the other seven functional groups in the data set we examined. The total biomass for plankton in each sample was obtained by adding the biomasses of the 8 functional groups. Monthly estimates were obtained by averaging all the samples collected in the same month.
9. Near the coast, SeaWiFS can overestimate the atmospheric correction, giving physically unrealistic negative reflectance values, particularly at 412 nm, the shortest wavelength. Negative radiance at 412 nm implies that the values at 510 and 555 nm are likely too small, so the ratio will tend to give chl-*a* values that are too large. As a consequence, a filter is typically used to remove negative radiance values. For coastal BC, we find that the average chl-*a* values for Negative Water Leaving Radiance filter "on" (NWLR-On) estimates are more similar to historical in-situ measurements of mean chl-*a* concentrations. However, comparison of the NWLR-On versus the NWLR-Off chl-*a* estimates for BC reveals that, while the NWLR-On estimates may represent more accurate estimates of the annual mean chl-*a* biomass, the NWLR-Off data yields more realistic estimates of the seasonal variability (i.e. spring and fall blooms) and the expected seasonal cycle in surface chl-*a* concentrations. The impression from our comparison is that the NWLR filter reduces high chl-*a* estimates too severely, and low chl-*a* estimates too conservatively. (See W.W. Gregg and N.W. Casey, *Remote Sensing of Environment* **93**, 463-479 (2004) for a comparison of SeaWiFS and observed chl-*a* data.)
10. For the mean chl-*a* data applied to the eleven NPFAC fishing regions in Table 1, we find the linear regression relation for the NWLR-On and NWLR-Off data to be: *chl-a*(NWLR-On) = 0.440 × *chl-a*(NWLR-Off)+0.523 with $r^2 = 0.96$ ($n = 11$; $p < 0.0001$). For all chlorophyll-a data (including the British Columbia data in Table 1), *chl-a*(NWLR-On) = 0.449 × *chl-a*(NWLR-off) + 0.487 with $r^2 = 0.98$ ($n = 17$; $p < 0.0001$).
11. Long-term fish catch data are available for the six fishing Regions in British Columbia (*5*) for the period 1920-91. The fisheries, particularly for groundfish, were still developing in BC prior to 1960. Therefore we calculated

the average, long-term catch of resident species for each region for the period 1960 to 1991 (Table 1). The long-term average yield (tonnes·km^{-2}) was estimated by dividing the catch by the surface area of each Region (see Supporting Online Material).
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13. Table 2 of C.E. Dorman and C.D. Winant (*J. Geophys. Res.* **100**, 16,029 (1995)) presents observed 10-year mean wind speeds for meteorological buoys moored along the west coast of the United States. Because of the Coriolis effect, winds blowing equatorward parallel to the west coast of North America generate a net seaward transport in the surface Ekman layer. This transport is compensated by a net onshore transport at depth, which gives rise to upwelling conditions over the continental slope.
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19. Because there are sufficient data to obtain reasonably accurate estimates of the average annual zooplankton and chl-*a* concentrations, we were able to divide the six BC fishing Regions into ten smaller sub-areas. The insert in Fig. 4a shows the relationship between these two variables ($Zoo = 33.9 \cdot (chl\text{-}a)^{0.531}$, adj. $r^2 = 0.81$; $p = 0.001$).
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23. We gratefully acknowledge the assistance of Jim Gower and John Wallace for providing us with SeaWiFs imagery from the DFO satellite facility, Lizette Beauchemin and Brian Wallace for processing the SeaWiFS data for the fish-catch areas, Don McQueen and Steve Romaine for assisting with the zooplankton data, Cynthia Wright and Patricia Kimber for helping prepare the manuscript, and Barbara Hickey who consulted with us on the validity of variously derived wind fields for the California coastal region. The comments provided by the three reviewers greatly improved the manuscript.

Supporting Online Material
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Materials and Methods
References and Notes

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Table 1. Mean annual chlorophyll concentrations (with temporal coefficients of variation, *cv*, shown in parentheses) and long-term annual yields of resident and highly migratory fish for various regions along the western continental margin of North America. Latitude denotes the central coastal location of each area. Migratory fish yields for Conception are not estimated because the fish stocks are distributed over a large, poorly defined area off southern California.

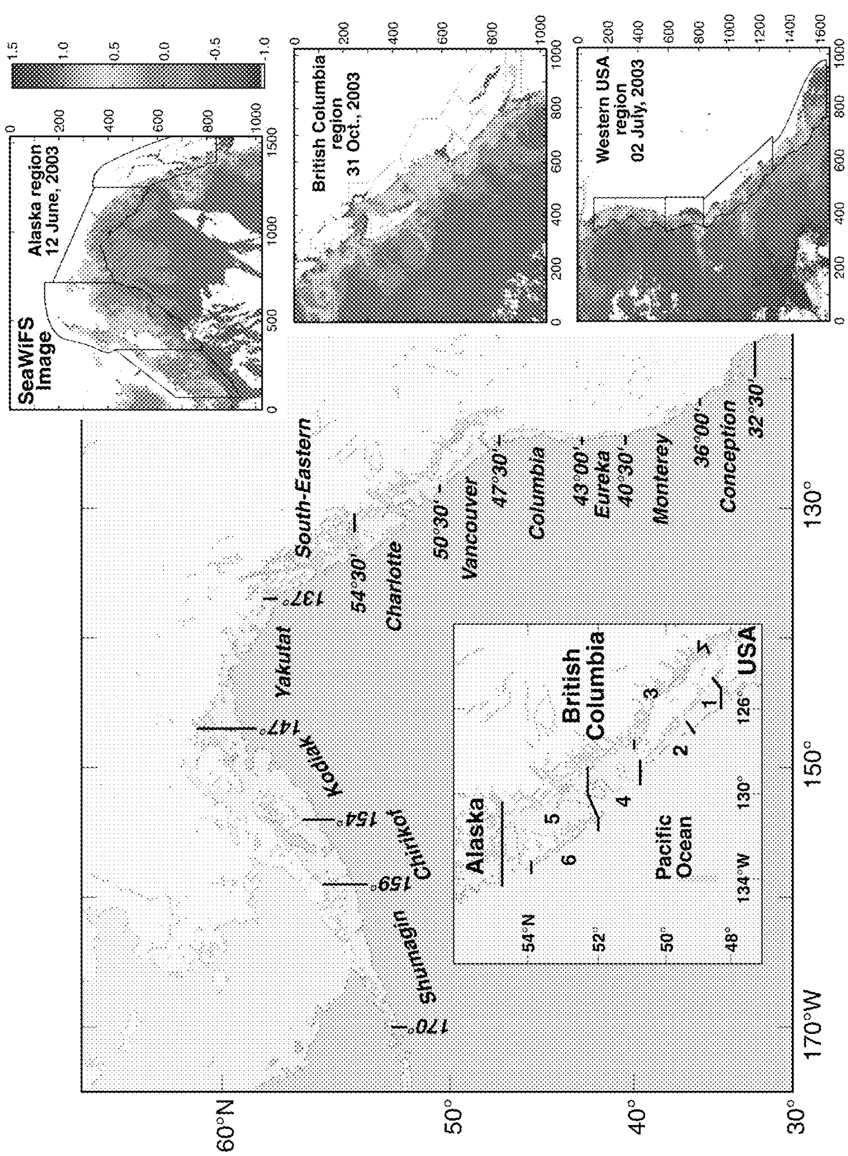
Region (latitude °N)	Surface Area [km^2]	Chl-*a* (NWLR-Off) [mg m^{-3}]	Chl-*a* (NWLR-On) [mg m^{-3}]	Resident fish yield [tonnes km^{-2}]	Migratory fish yield [tonnes km^{-2}]	Total fish yield [tonnes km^{-2}]
Part A: NPAFC Areas						
Conception (34.3°N)	60,046	1.38 (0.57)	1.06 (0.44)	0.06	.	.
Monterey (38.3°N)	41,613	2.29 (0.54)	1.42 (0.40)	0.45	0.39	0.84
Eureka (41.8°N)	18,692	2.20 (0.86)	1.47 (0.66)	0.66	0.88	1.54
Columbia (45.3°N)	36,573	3.24 (0.68)	2.02 (0.60)	0.88	2.65	3.53
Vancouver (49.0°N)	34,688	5.15 (0.66)	2.81 (0.57)	1.97	1.43	3.40
Charlotte (52.5°N)	82,769	2.16 (0.69)	1.45 (0.53)	0.79	0.01	0.80
SE Alaska (56.1°N)	43,342	2.79 (0.80)	1.62 (0.52)	0.60	0	0.60
Yakutat (58.5°N)	76,430	1.57 (0.63)	1.39 (0.43)	0.27	0	0.27
Kodiak (57.4°N)	144,911	2.00 (0.62)	1.50 (0.43)	0.63	0	0.63
Chirikof (54.9 °N)	83,590	1.83 (0.79)	1.35 (0.55)	0.65	0	0.65
Shumagin (53.3°N)	116,074	1.66 (1.20)	1.21 (0.84)	0.36	0	0.36
Part B: British Columbia						
BC F1 (48.5 °N)	11,312	4.26 (0.70)	2.48 (0.62)	2.39	2.93	5.32
BC F2 (49.6 °N)	10,099	3.30 (0.71)	1.91 (0.63)	0.85	0	0.85
BC F3 (49.4 °N)	8,803	6.92 (0.57)	3.56 (0.47)	3.19	0	3.19
BC F4 (51.6 °N)	31,408	2.00 (0.71)	1.34 (0.55)	0.92	0.03	0.95
BC F5 (53.1 °N)	44,158	2.41 (0.68)	1.61 (0.48)	0.80	0	0.80
BC F6 (53.0 °N)	7,203	1.10 (0.69)	0.86 (0.56)	1.03	0	1.03

Fig. 1. Map of the eleven NPAFC regions extending from "Conception" off California to "Shumagin" off western Alaska. Inset in the ocean shows the areas covered by the six British Columbia sub-regions. Insets on land are examples of daily SeaWiFS chl-*a* maps for the Alaska, British Columbia and western U.S. regions; grids are in pixels, at 1.1 km/pixel, and the color bar denotes concentration in log(chl-*a* in mg·m^{-3}).

Fig. 2. Large-scale trophic linkage between the annual mean chl-*a* concentration (NWLR filter "Off") and the long-term annual yield of resident fish for each of the eleven NPAFC regions. Solid circles denote upwelling regimes, open circles downwelling regimes.

Fig. 3. South-to-north variation in (black bars) the mean annual seaward component of accumulative Ekman transport from (http://www.pfeg.noaa.gov) using positive (upwelling) values only, and (white bars) the mean annual chl-*a* concentration from SeaWiFS averaged over the scale of the NPAFC regions. Observations span the period January 1998 to December 2003. Connected circles are the 10-year mean components of the alongshore wind speed from coastal meteorological buoys along the west coast of the United States taken from Table 2 of Dorman and Winant (*13*). Mean winds are roughly alongshore (equatorward) except for the three sites north of 44° N where mean annual winds are predominantly poleward. The especially low wind speed at 33°42' is for buoy NDBC 25 located well within the sheltered region of the Southern California Bight (SCB).

Fig. 4. Small-scale trophic linkages for each of the six British Columbia sub-regions. (A) Linkage between the mean annual concentrations of chl-*a* and zooplankton, and (B) the corresponding linkage between mean annual zooplankton biomass and the long-term mean annual resident fish yield. The insert in the top panel shows an almost identical relationship when the BC zooplankton and chl-*a* data are analyzed at an even smaller-spatial scale. SoG denotes the value for the Strait of Georgia (BC F3).



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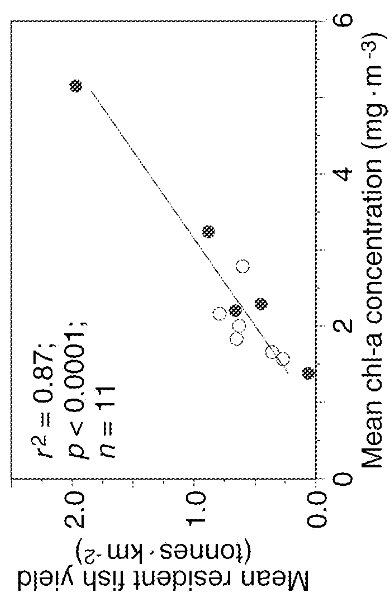

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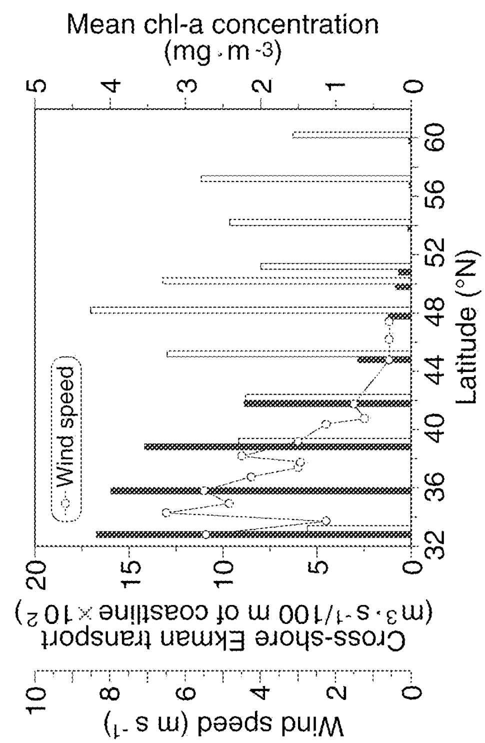

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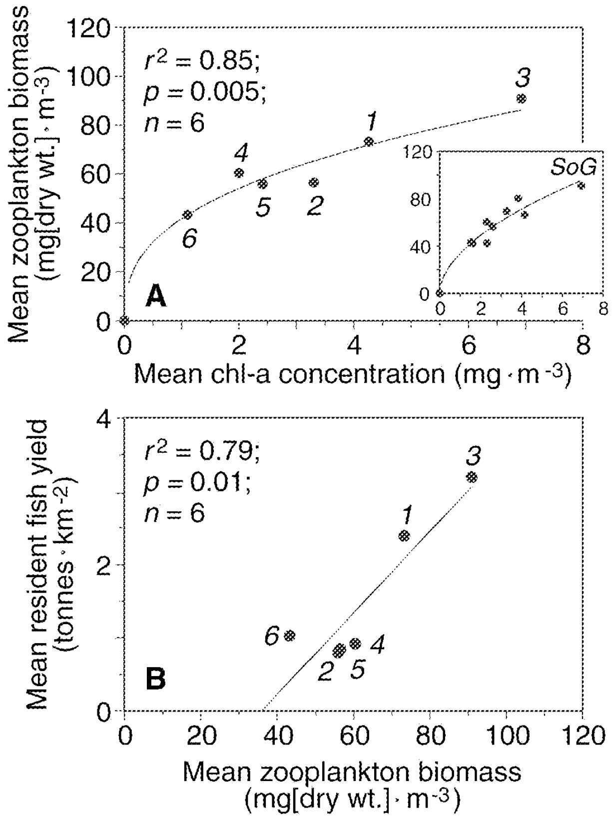

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