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

Daniel M. Ware^{1,2,3} and Richard E. Thomson^{4,2,5*}

We addressed the question of bottom-up versus top-down control of marine ecosystem trophic interactions by 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. The 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 phytoplankton, zooplankton, and resident fish, extending to regional areas as small as 10,000 square kilometers.

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, including fisheries (top-down processes). Comparative cross-system analy-

ses (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). Although it is certain that, at some high harvest level, a fishery will begin to exert a controlling influence on fish production, the rate of removal at which this level occurs is uncertain. We used satellite-derived estimates of mean annual chlorophyll *a* (chl-*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 chl-*a* concentration (Fig. 1), a proxy measure of the

surface phytoplankton concentration (3), are available at a spatial resolution of 1.1 km through 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). At the larger spatial scales examined in this study (average surface area, 67,157 km²), we calculated the mean annual chl-*a* concentrations for the years 1998 to 2003 for the 11 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 and Fig. 1). We also calculated smaller scale (average area, 18,830 km²) mean concentrations for six oceanographically distinct fishing areas identified (7) for western British Columbia (Fig. 1). Extensive zooplankton time series for British Columbia (8) further made it possible to examine regional-scale trophic coupling between phytoplankton and zooplankton and between zooplankton and fish.

The mean chl-*a* values used in this study are those for which the negative water leaving radiance (NWLRL) filter (9) was not applied (NWLRL-Off). For the regions we studied, 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 metric tons per km²) of resident and highly migratory fish species for the northeast Pacific continental margin were calculated from long-term

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Table 1. Mean annual chl-*a* concentrations (with temporal coefficients of variation 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- <i>a</i> (NWLRL-Off) (mg m ⁻³)	Chl- <i>a</i> (NWLRL-On) (mg m ⁻³)	Resident fish yield (metric tons km ⁻²)	Migratory fish yield (metric tons km ⁻²)	Total fish yield (metric tons km ⁻²)
<i>NPAFC Areas</i>						
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
Southeast 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
<i>British Columbia</i>						
BCF1 (48.5°N)	11,312	4.26 (0.70)	2.48 (0.62)	2.39	2.93	5.32
BCF2 (49.6°N)	10,099	3.30 (0.71)	1.91 (0.63)	0.85	0	0.85
BCF3 (49.4°N)	8,803	6.92 (0.57)	3.56 (0.47)	3.19	0	3.19
BCF4 (51.6°N)	31,408	2.00 (0.71)	1.34 (0.55)	0.92	0.03	0.95
BCF5 (53.1°N)	44,158	2.41 (0.68)	1.61 (0.48)	0.80	0	0.80
BCF6 (53.0°N)	7,203	1.10 (0.69)	0.86 (0.56)	1.03	0	1.03

landing statistics compiled by the International North Pacific Fisheries Commission (INPFC) and NPAFC for the period 1960 to 1998. For the six British Columbia 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 that 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 1 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 11 large-scale NPAFC statistical areas spanning western North America. Biweekly chl-a concentrations were 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 , in metric tons km^{-2}) and the mean annual chl-a concentration (in mg m^{-3}), such that $LTY = 0.436 \times \text{chl-a}(\text{NWLR-Off}) - 0.38$, with adjusted squared correlation coefficient $r^2 = 0.87$. 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 revealed that neither the type of domain nor the domain-chlorophyll interaction effects were 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, which is forced by 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). Coincidentally, 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

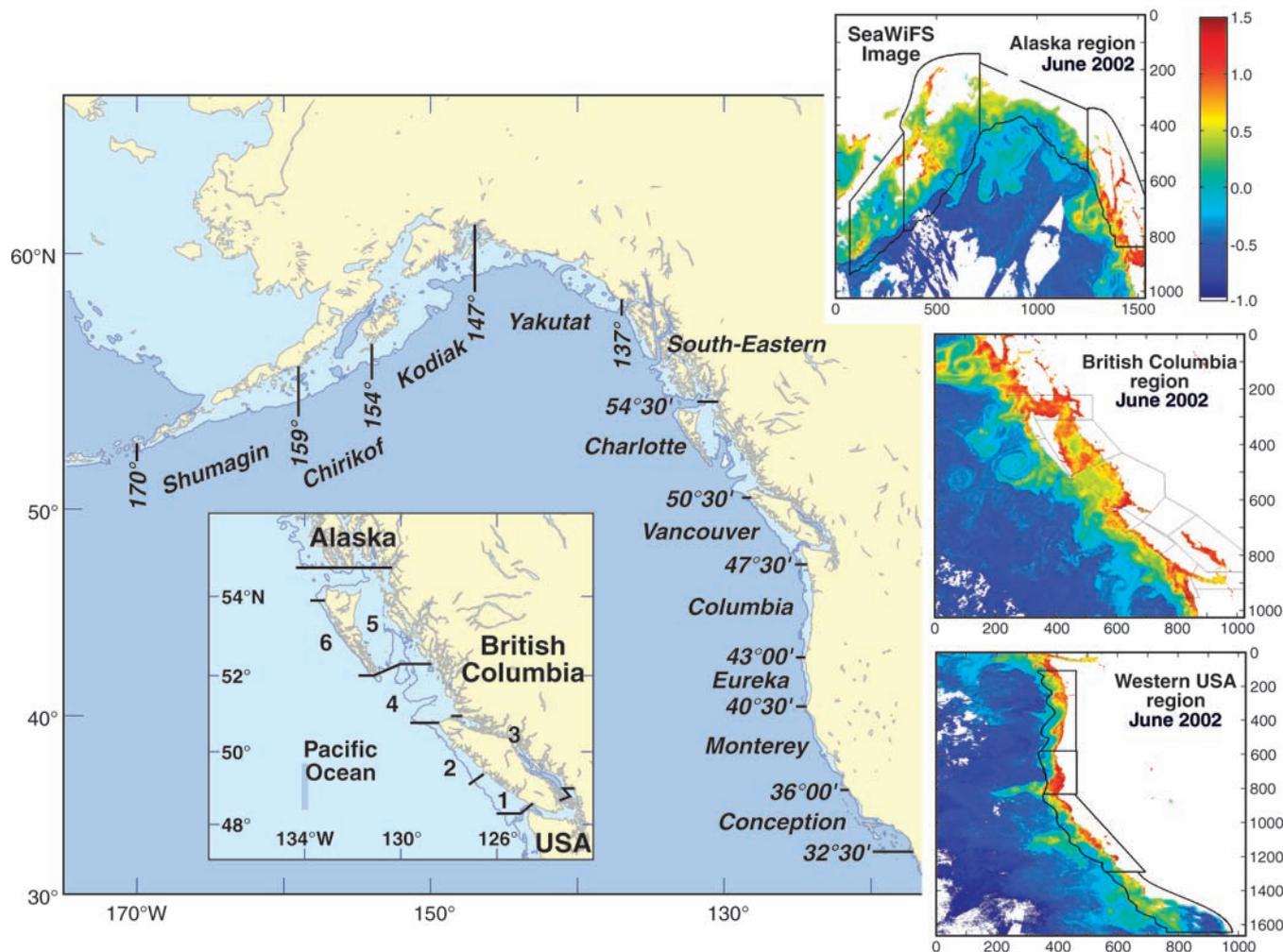


Fig. 1. Map of the 11 NPAFC regions, extending from Conception off California to Shumagin off western Alaska. (Left inset) The areas covered by the six British Columbia subregions. (Right insets) Examples of monthly

mean SeaWiFS chl-a maps for the Alaska, British Columbia, and western U.S. regions; grids are in pixels, at 1.1 km/pixel ; the color bar denotes concentration in $\log(\text{chl-a in } \text{mg m}^{-3})$.

regions negatively correlated ($P = 0.011$) with the annual cumulative seaward Ekman transport. The negative sign of this correlation is counterintuitive (in that decreasing seaward Ekman transport is normally thought to produce reduced primary productivity) and indicates that factors other than wind-induced upwelling are important for plankton productivity. For example, from 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 substantial 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-*a* concentrations occur in the Washington–southern British Columbia region, where there is moderate upwelling and substantial year-round freshwater flux (from the Columbia and Fraser rivers). The latter provides both stability and micronutrients. The continental margin off the British Columbia–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 fresh water entering the coastal ocean from major rivers continues to be a major source of micronutrients and upper ocean stability (16, 17). Macronutrients are supplied through current-induced upwelling, coastal eddies, and winter upwelling winds. Thus, chl-*a* 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. The largest hake catches occur between 42°N and 50°N (Table 1), which is also the region of the 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 for migratory species 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 British Columbia 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), and the lowest concentrations were in areas BCF4 and BCF6 off the outer northwest coast (Fig. 1 and Table 1). Biweekly 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, BCF2, and BCF4) (Table 1).

As with the NPAFC regions, the smaller scale British Columbia regions show a significant linear correlation between the mean annual chl-*a* concentration (mg m^{-3}) and the mean annual resident fish yield (metric tons km^{-2}), with $LTY = 0.437 \times \text{chl-}a(\text{NWLR-Off}) + 0.08$, with adjusted $r^2 = 0.76$ ($P = 0.015$) (Table 1). 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-*a* regression for the large-scale NPAFC areas (Fig. 2).

Zooplankton abundance time series for coastal British Columbia enabled us to extend our analysis to 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 British Columbia regions are highly correlated through the power-law function $Zoo = 46.57 \times (\text{chl-}a)^{0.488}$, with adjusted $r^2 = 0.85$; here, Zoo denotes zooplankton concentration (in mg of dry weight per m^3) and the mean chlorophyll concentration (NWLR Filter-Off) is in mg m^{-3} . This relationship is nonlinear, presumably 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 sea floor and is ultimately transferred to the shelf fish community through the benthic food web. The relationship between resident fish yield and zooplankton in British Columbia is linear (Fig. 4B): $LTY = 0.055 \times Zoo - 1.98$, with adjusted $r^2 = 0.79$ ($n = 6$ catch areas, $P = 0.01$). Small zooplankton are an important

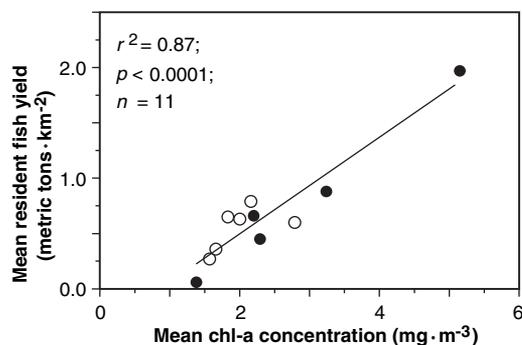


Fig. 2. Large-scale trophic linkage between the annual mean chl-*a* concentration (NWLR-Off) and the long-term annual yield of resident fish for each of the 11 NPAFC regions. Solid circles denote upwelling regimes; open circles, downwelling regimes.

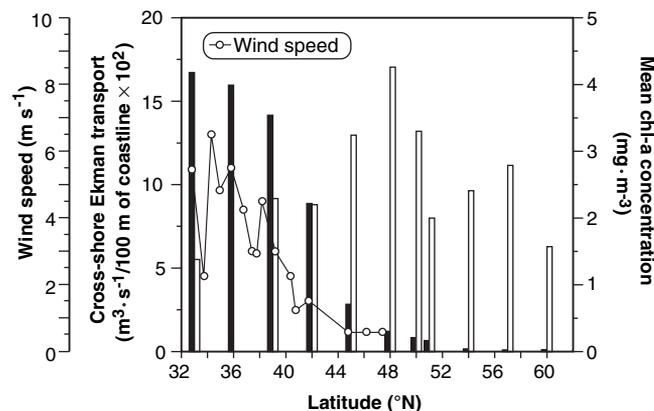


Fig. 3. South-to-north variation in the mean annual seaward component of accumulative Ekman transport (30) given positive (upwelling) values only (black bars) and the mean annual chl-*a* concentration from SeaWiFS (white bars), averaged over the scale of the NPAFC regions. Observations span the period January 1998 to December 2003. Connected circles represent 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 (29). 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 National Data Buoy Center 25, located well within the sheltered region of the Southern California Bight.

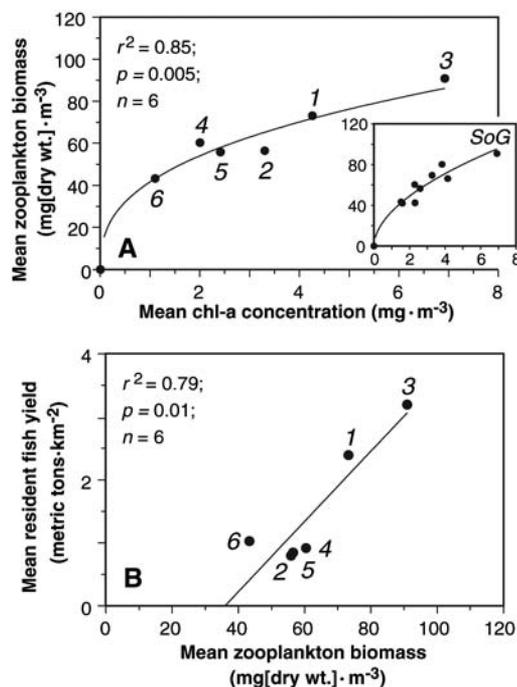
food source for the early life history stages of all resident fish species, and larger zooplankton are an important food for many juvenile and adult resident fish.

Our analysis leads to several fundamental conclusions concerning marine food web interactions along the west coast of North America. Within the large-scale (67,000 km²) NPAFC 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) produced high fishery yields. Plankton and fisheries data for coastal British Columbia further reveal that this linkage also extends to much smaller spatial scales (19,000 km²). Regression of the long-term, averaged, resident fish yield against chl-a concentration yielded the same regression slope for both the coastal upwelling and coastal downwelling domains, a highly unexpected result because the biological diversities of the zooplankton and the migratory and resident fish communities in these domains are quite distinct. The similar regression 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 found that the resident fish yields in summer upwelling regions increase poleward, in inverse proportion to the annual accumulative Ekman transport seaward over the continental margin, and reach a maximum in southern British Columbia near the north-

ern 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 and 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 Alaskan coast, despite the absence of substantial coastal upwelling. Consequently, the tightly coupled phytoplankton-fish relationship we observed for the west coast of North America must be maintained by either an onshore nutrient supply, late-winter “preconditioning” of the surface ocean (20), 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 region indicates that 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 Richardson and Schoeman (22), who found that an increase in water temperatures in warmer regions in the northeast Atlantic leads to a decrease in phytoplankton abundance.

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. (Inset) An almost identical relationship appears when the British Columbia zooplankton and chl-a data are analyzed at an even smaller spatial scale. SoG denotes the value for the Strait of Georgia (BCF3). (B) The corresponding linkage between mean annual zooplankton biomass and the long-term mean annual resident fish yield.



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- Satellite-based phytoplankton pigment (chl-a) estimates were derived from water-leaving radiance at near-infrared frequency bands after correction for atmospheric optical properties (23). Except for highly turbid coastal waters, where the optical properties of inorganic suspended matter and colored dissolved organic matter can be problematic (24), the calibrated radiance data are a proxy for surface phytoplankton concentration.
- Chl-a concentrations were 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.
- In the Columbia region, the depth-integrated daily rate of primary production is linearly correlated with the surface chl-a concentration (15).
- Long-term average fish catches were compiled from data summarized in the INPFC/NPAFC statistical yearbooks for the period 1960 to 1998 (25) and in the California Cooperative Oceanic Fisheries Investigations report series. The catch time series indicate 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, developed 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 mackerel 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, a substantial fraction of the total catch in this region consisted of highly migratory species (Table 1). 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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- Monthly mean estimates of total zooplankton concentrations (mg of dry weight per m³) were derived for the six coastal regions in British Columbia. The data (mostly collected between 1992 and 2002) were obtained from the Institute of Ocean Sciences in Sidney, British Columbia (26). The raw data were sorted into bins according to the coastal region where the samples were collected. The original 53 zooplankton species groups were reduced to eight functional groups. An analysis of variance indicated a highly significant night-day sampling effect for euphausiids: Euphausiid night biomasses were 2.8 to 5.4 times higher than day biomasses. The night/day ratio was species-specific. Accordingly, we corrected euphausiid samples collected during the day by multiplying the day biomass by the species-specific night/day correction factor. We found no significant day-night sampling effect on the other seven functional groups in our data set. We obtained the total biomass for plankton in each sample by adding the biomasses of the eight functional groups and obtained monthly estimates by averaging all the samples collected in the same month.
- 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 British Columbia, we found that the average chl-a values for 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 British Columbia reveals that, although the NWLR-On data may represent more accurate es-

- imates of the annual mean chl-a biomass, the NWLR-Off data yield more realistic estimates of the seasonal variability (i.e., spring and fall blooms) and the expected seasonal cycle in surface chl-a concentrations. This comparison implies that the NWLR filter eliminates high chl-a estimates too severely and retains low chl-a estimates too conservatively (27).
- For the mean chl-a data applied to the 11 NPFAC fishing regions in Table 1, we found the linear regression relation for the NWLR-On and NWLR-Off data to be $chl-a(NWLR-On) = 0.440 \times chl-a(NWLR-Off) + 0.523$, with $r^2 = 0.96$ ($n = 11$ regions; $P < 0.0001$). For all chl-a data (including the British Columbia data in Table 1), $chl-a(NWLR-On) = 0.449 \times chl-a(NWLR-Off) + 0.487$ with $r^2 = 0.98$ ($n = 17$, all fishing regions; $P < 0.0001$).
 - Long-term fish catch data are available for the six fishing regions in British Columbia (7) for the period 1920 to 1991. The fisheries, particularly for groundfish, were still developing in British Columbia before 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 (metric tons km^{-2}) was estimated by dividing the catch by the surface area of each region (28).
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 - 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 British Columbia fishing regions into 10 smaller subareas. The inset in Fig. 4A shows the relationship between these two variables [$Zoo = 33.9 \times (chl-a)^{0.531}$, adjusted $r^2 = 0.81$; $P = 0.001$].
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- Time series of Ekman transport are available from the Pacific Fisheries Environmental Laboratory at www.pfeg.noaa.gov.
- We thank J. Gower and J. Wallace for providing us with SeaWiFS imagery from the Department of Fisheries and Oceans satellite facility, L. Beauchemin and B. Wallace for processing the SeaWiFS data for the fish catch areas, D. McQueen and S. Romaine for assisting with the zooplankton data, C. Wright and P. Kimber for helping prepare the manuscript, B. Hickey for consulting with us on the validity of variously derived wind fields for the California coastal region, and three reviewers for comments on the manuscript.

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References and Notes

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An Asymmetric Energetic Type Ic Supernova Viewed Off-Axis, and a Link to Gamma Ray Bursts

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Type Ic supernovae, the explosions after the core collapse of massive stars that have previously lost their hydrogen and helium envelopes, are particularly interesting because of their link with long-duration gamma ray bursts. Although indications exist that these explosions are aspherical, direct evidence has been missing. Late-time observations of supernova SN 2003jd, a luminous type Ic supernova, provide such evidence. Recent Subaru and Keck spectra reveal double-peaked profiles in the nebular lines of neutral oxygen and magnesium. These profiles are different from those of known type Ic supernovae, with or without a gamma ray burst, and they can be understood if SN 2003jd was an aspherical axisymmetric explosion viewed from near the equatorial plane. If SN 2003jd was associated with a gamma ray burst, we missed the burst because it was pointing away from us.

When a massive star reaches the end of its life and exhausts its nuclear fuel, the core itself collapses to form a compact remnant (a neutron star or a black hole). Although the exact mechanism is not well understood, the resulting release of energy leads to the ejection of the envelope of the star at high velocities, producing a supernova (SN).

Typically, a massive star has a large H-rich envelope, making it difficult to observe the innermost part, where the action takes place. However, there are some cases where the H envelope, and also the inner He envelope, were lost before the star exploded, through either a stellar wind or, more likely, binary interaction (1). These SNe, called type Ic, offer a view

close to the core, and so they are particularly interesting as tools to study the properties of the collapse and of the SN ejection.

Some type Ic SNe, characterized by a very high kinetic energy (2, 3), have been observed to be linked with the previously unexplained phenomenon of gamma ray bursts (GRBs), which are brief but extremely bright flashes of hard (γ -ray and x-ray) radiation that had baffled astronomers for decades (4–8). The link between type Ic SNe and GRBs is probably not accidental. If a jet is produced by a collapsing star, it can only emerge and generate a GRB if the stellar envelope does not interfere with it (9).

In view of this link, we have searched among known type Ic SNe for the counterpart of a property that is typical of GRBs: asphericity. A jet-like explosion is required for GRBs from energetics considerations; if they were spherically symmetric, GRBs would involve excessively large energies, comparable to the rest mass of several suns. The best evidence for asphericity in the GRB-associated SNe (GRB/SNe) to date has come from the fact that iron seems to move faster than oxygen in the ejected material. Evidence of this is seen in spectra obtained several months after the explosion, when the ejected material has decreased in density and behaves like a nebula. The GRB/SN 1998bw (10) showed strong emission lines of [O I] (a forbidden line of neutral oxygen), as do normal type Ic SNe, but also of [Fe II] (a forbidden line of singly ionized iron), which are weak in normal type Ic SNe. The [Fe II] lines near 5100 Å in SN 1998bw are broader than the [O I] 6300 and 6363 Å blend.