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An Ecosystem Services Perspective for the Oceanic Eastern Tropical Pacific: Commercial Fisheries, Carbon Storage, Recreational Fishing, and Biodiversity

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The ocean provides ecosystem services (ES) that support humanity. Traditional single-issue management largely failed to protect the full suite of ES. Ecosystem-based management (EBM) promotes resilient social-ecological systems that provide ES. To implement EBM, an ES approach is useful: (1) characterize major ES provided (magnitude, geographic extent, monetary value, trends, and stakeholders), (2) identify trade-offs, (3) determine desired outcomes, and (4) manage anthropogenic activities accordingly. Here we apply the ES approach (steps 1–2) to an open ocean ecosystem, the eastern tropical Pacific (ETP), an area of 21 million km^2 that includes waters of 12 nations and the oceanic commons, using 35 years (1975–2010) of fisheries and economic data, and 20 years (1986–2006) of ship-based survey data. We examined commercial fisheries, carbon storage, recreational fishing, and biodiversity as the major provisioning, regulating, cultural, and supporting ES, respectively. Average catch value (using U.S. import prices for fish) for the 10 most commercially fished species was $2.7 billion yr^{-1}. The value of carbon export to the deep ocean was $12.9 billion yr^{-1} (using average European carbon market prices). For two fisheries-depleted dolphin populations, the potential value of rebuilding carbon stores was $1.6 million (cumulative); for exploited fish stocks it was also $1.6 million (an estimated reduction of 544,000 mt). Sport fishing expenditures totaled $1.2 billion yr^{-1}, from studies of three popular destinations. These initial, conservative estimates do not represent a complete summary of ETP ES values. We produced species richness maps for cetaceans, seabirds, and ichthyoplankton, and a sightings density map for marine turtles. Over 1/3 of cetacean, seabird, and marine turtle species occur in the ETP, and diversity (or density) hotspots are widespread. This study fills several gaps in the assessment of marine and coastal ES by focusing on an oceanic habitat, utilizing long-term datasets, mapping the spatial distribution of ecological components, and concentrating on an area beyond Europe and the USA.

Our results improve our understanding of ETP ES, highlight their variety, and offer a new perspective for a fisheries-dominated system. This study sets the stage for further analyses of trade-offs, which can inform decisions about resource management and biodiversity conservation.

INTRODUCTION

The ocean provides ecosystem services (ES) that are critical to the survival and well-being of humanity (Ehrlich and Ehrlich, 1981; Costanza et al., 1997; Daily et al., 1997; Costanza, 1999). Defined as material and non-material benefits (i.e., goods and services) that people derive from the planet's ecological processes (Ehrlich and Ehrlich, 1981; Costanza et al., 1997; Daily et al., 1997; Fisher et al., 2009), ES vary in nature and scale, and are commonly categorized into four groups: (1) provisioning (e.g., production of food, fuel, or water), (2) regulating (e.g., regulation of climate, floods, or disease), (3) supporting (e.g., nutrient cycling, oxygen production, or habitat creation), and (4) cultural (e.g., recreational, spiritual, or aesthetic uses) (Millenium Ecosystem Assessment, 2003). Key examples from the ocean highlight the magnitude and importance of its ES. First, it *provisions* a major food source—nearly 4.3 billion people obtain 15% of their animal protein from fish, two-thirds of which comes from the ocean (105 million metric tons (mt) annually) (UNFAO, 2014). Second, the ocean *regulates* climate by serving as a major carbon sink—it has absorbed 41% of all anthropogenic carbon emissions (Sabine and Tanhua, 2010), thereby dampening the warming of the terrestrial biosphere. Third, marine organisms, most notably phytoplankton, account for nearly 50% of global primary production (Field et al., 1998)—this *supports* marine ecosystems by generating oxygen and particulate organic carbon (POC) for animals to consume. This process also initiates the biological pump, which transports a fraction of POC from the surface to the deep ocean, where it is sequestered on timescales of thousands to millions of years (Ducklow et al., 2001; Henson et al., 2012). Finally, the ocean provides a multitude of *cultural* services, including recreational opportunities (e.g., boating, diving, fishing, and surfing) and spiritual, artistic, historical, and educational information (de Groot et al., 2002)—these have been important throughout human history and in recent decades have made marine tourism the fastest growing tourism sector in the world (Hall, 2001). Globally, the economic value of all marine ES is estimated at $50 trillion (USD) yr^{-1} (Costanza et al., 2014).

There are trade-offs among competing uses of ocean resources, making it important to measure the value of ES accurately so that trade-offs can be made explicit (i.e., the resources can be managed to maximize the total economic value of these services). Because these trade-offs historically have been (and are often still) ignored, some resources have been over-exploited by human activities, leading to a reduction in the total economic value provided by all ocean resources. For example, impacts from overfishing, habitat destruction, pollution, and anthropogenic climate change (Jackson et al., 2001; Dulvy et al., 2003; Pandolfi et al., 2003; Worm et al., 2005, 2006; Lotze et al., 2006; Halpern et al., 2008) have resulted from decisions to exploit valuable resources (e.g., fish or crude oil) without considering negative externalities (e.g., loss of biodiversity or global warming). For extractive commodities that are either common resources or public goods without property rights, ignoring trade-offs has sometimes led to exploitative races resulting in the "tragedy of the commons" (Hardin, 1968). In many cases, the cumulative effects of ignoring ES trade-offs have degraded ecosystems, decreased biodiversity, and diminished the capacity of marine ecosystems to support increasing human populations (Worm et al., 2006).

The predominant twentieth century approach to marine resource management failed to adequately protect living resources from human impacts, resulting in widespread calls for a new management paradigm at the turn of the century (Pikitch et al., 2004; McLeod et al., 2005; Arkema et al., 2006). The traditional focus on single sectors, species, and activities did not account for the complex interaction of ecological, social, economic, and political factors impacting natural resources. Reliance on single disciplines of expertise resulted in a piece-meal understanding of marine ecosystems. Ecosystem-based management (EBM) was proposed as an alternative, holistic approach which considers the entire system, rather than single sectors or species, and explicitly factors humans into the equation (Pikitch et al., 2004; McLeod et al., 2005; Arkema et al., 2006). At its core is the goal of maintaining healthy, productive, and resilient ecosystems that will provide the services that humans want and need into the future (Pikitch et al., 2004; McLeod et al., 2005). To accomplish this goal, an ES approach can be employed in four broad steps: (1) characterize key ES provided by the system that are valuable to society in some way, (2) identify and understand the trade-offs associated with each service, (3) determine the desired outcomes for the system in terms of the level of each service to maintain, and (4) manage anthropogenic activities to achieve the desired outcomes.

The ES approach requires an understanding of the social-ecological system of interest, and is critical to implementation of EBM; however, its application in the marine environment has been largely limited to coastal systems, particularly mangroves, wetlands, and coral reefs (see Liquete et al., 2013 for a review of marine and coastal ES studies). This is apparent in the number of monetary value estimates that exist for coastal systems: of 275 estimates, 95% were relevant to coastal marine systems and only 5% pertained to the open ocean (de Groot et al., 2012). There has been much less emphasis on the open ocean because it is remote, and significantly more difficult to study and manage. However, as the management paradigm for open ocean ecosystems moves

toward more holistic approaches, efforts to assess their ES will need to progress.

The goal of this paper is to apply the ES approach to an open ocean system (i.e., an ecosystem seaward of the continental shelf, which we will refer to as "oceanic"). Using long-term fisheries, economic, and ship-based research survey datasets, we tackle the first two steps listed above by (1) characterizing the major ES in terms of their magnitude, geographic extent, monetary value (where appropriate), trends in quantities and values, and stakeholders, and (2) identifying potential trade-offs among those ES. We use the eastern tropical Pacific (ETP) as a case study and target (1) commercial fisheries as a provisioning service, (2) carbon storage as a regulating service, (3) recreational (sport) fishing as a cultural service, and (4) biodiversity as a supporting service. While the benefits of commercial and recreational fishing are direct (e.g., food and recreation) and familiar to most, the benefits of carbon storage and biodiversity warrant further introduction.

Carbon storage is important due to its role in mitigating anthropogenic climate change (Sabine and Tanhua, 2010). The uptake of CO_2 at the ocean surface is primarily influenced by physical and chemical processes (Sabine and Tanhua, 2010). Some regions of the ocean are sources of atmospheric CO_2, while others are sinks (Takahashi et al., 2009; Khatiwala et al., 2013). For the ETP, one study of global sea-air CO_2 flux dynamics concluded it was a source (Takahashi et al., 2009), while another study using global repeat hydrography to estimate CO_2 storage rates concluded that it was a sink (Khatiwala et al., 2013). However, regardless of whether the ETP is a source or sink of atmospheric CO_2, there are biological processes beneath the surface that influence the production, distribution, and storage of organic carbon. The biological pump moves POC from the surface to deep ocean sediments through passive (e.g., sinking fecal pellets and ballasts) and active (e.g., vertical migrations by fish and zooplankton) transport (Eppley and Peterson, 1979; Ducklow et al., 2001; Henson et al., 2012; Davison et al., 2013). Additionally, carbon is stored in populations of large, long-lived vertebrates (e.g., apex predators), such as cetaceans and large fish; this is comparable to carbon being stored in large trees (Pershing et al., 2010). These important regulating services can be impacted by the use of provisioning services, particularly fisheries, which have the capacity to reduce populations of large consumer species and alter food web structure (Dayton et al., 1995; Jackson et al., 2001; Pauly et al., 2002). Such changes may decrease the amount of carbon stored in megafauna populations and alter the magnitude and efficiency of the biological pump, which is strongly influenced by food web structure (Ducklow et al., 2001; Pershing et al., 2010).

Biodiversity is important because of its link to ecosystem resilience, "the extent to which ecosystems can absorb recurrent natural and human perturbations and continue to regenerate without slowly degrading or unexpectedly flipping into alternate states" (Hughes et al., 2005). The role of biodiversity in ecosystem resilience has been a long-standing theme in ecology (Holling, 1973; Levin and Lubchenco, 2008). Theoretically, resilience is enhanced when functional groups comprise ecologically redundant species, each of which responds differently to
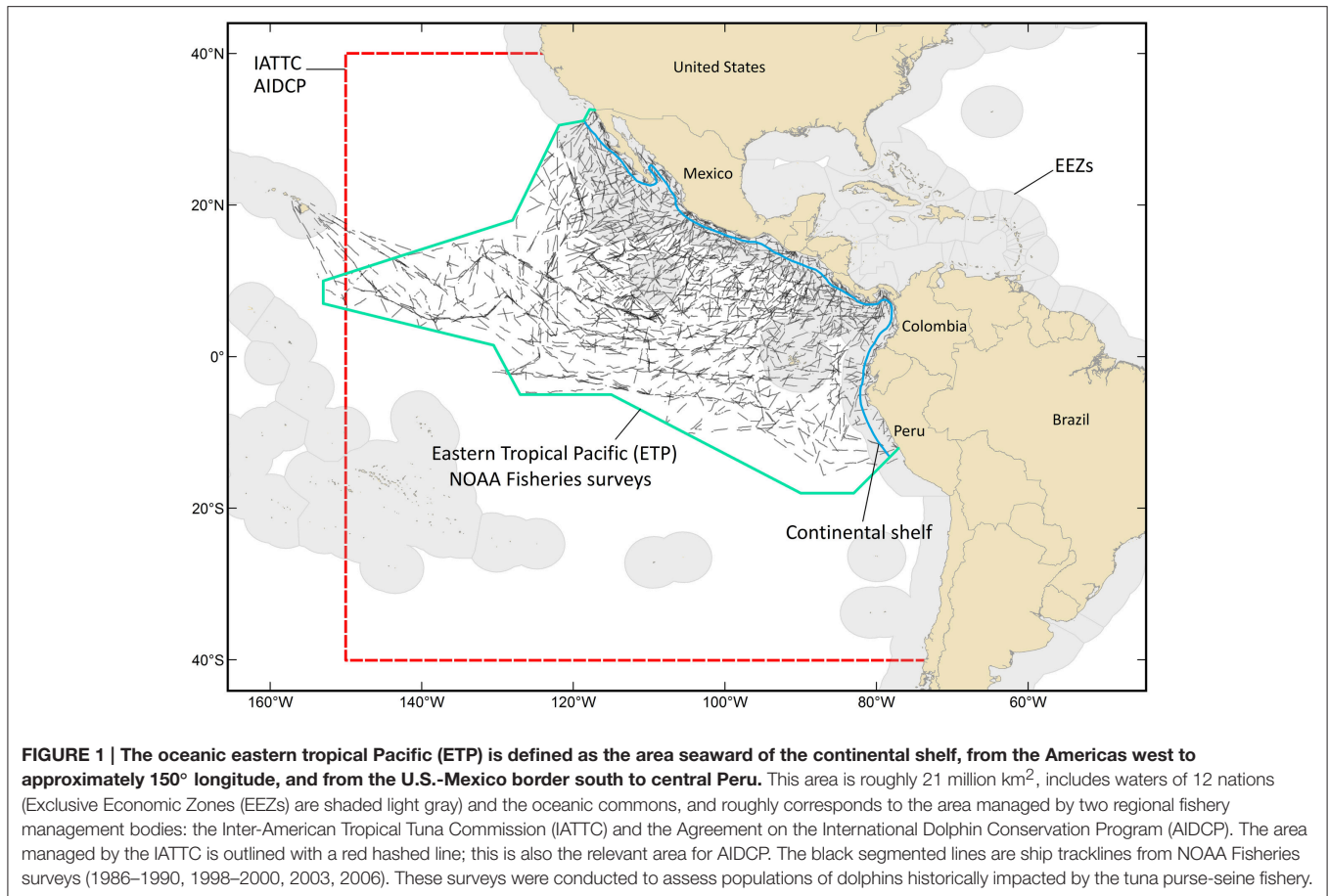
environmental changes (Walker, 1995). If one species is depleted, another will assume the same functional role. Thus a higher number of species insures against ecosystem collapse in the face of environmental fluctuation (Yachi and Loreau, 1999; Loreau et al., 2001). Indeed, marine ecosystems with fewer species are often functionally compromised, and those with more species are more likely to have functional redundancy (Steneck et al., 2002, 2004; Bellwood et al., 2004; Hughes et al., 2005). For example, studies showed that species-rich kelp forests off the west coast of North America are more resilient than naturally species-poor kelp forests off the east coast (Steneck et al., 2002, 2004). However, a higher number of species would not confer resilience if the species had similar responses to external pressures, such as overfishing and pollution (Chapin et al., 1997; Folke et al., 2004; Hughes et al., 2005). Thus, diversity of functional groups, diversity of species in functional groups, and diversity within species and populations all appear to be critical for the production and resilience of ES (Chapin et al., 1997; Luck et al., 2003; Folke et al., 2004).

This case study provides an initial, conservative assessment of key ES provided by the ETP. It is limited in scope by the availability of data and therefore does not represent a complete summary of all ETP ES and their values. This study fills several gaps in the assessment of marine and coastal ES (Liquete et al., 2013) by focusing on an oceanic habitat, utilizing long-term datasets to produce an assessment, mapping the spatial distribution of ecological components, and concentrating on an area beyond Europe and North America (particularly the USA). Our results highlight the variety of ES provided by the ETP and offer a new perspective for a socio-ecological system that historically has had commercial tuna fisheries at its core. By improving our understanding of ETP ES, this study sets the stage for further analyses of trade-offs, which can inform decisions about resource management and biodiversity conservation.

METHODS

Study Area

We define the oceanic ETP as the area seaward of the continental shelf, from the Americas west to approximately 150° longitude, and from the U.S.-Mexico border south to central Peru (**Figure 1**). It has an area of 21 million km^2, includes waters of 12 nations and the oceanic commons, and roughly corresponds to the area managed by two regional fishery management bodies: the Inter-American Tropical Tuna Commission (IATTC) and the Agreement on the International Dolphin Conservation Program. The ETP has been among the world's most productive fishing grounds for yellowfin, bigeye, and skipjack tuna (*Thunnus albacares*, *T. obesus*, and *Katsuwanus pelamis*, respectively) for more than 50 years. The commercial tuna purse-seine fishery has a long history of negative incidental impacts on pantropical spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris,* respectively; Wade et al., 2007); the western boundary of the ETP study area (**Figure 1**) is the western range limit for the impacted stocks of these species. Because of the magnitude of the commercial fishery and the historical impacts on dolphin populations, the ETP has been well-studied

FIGURE 1 | The oceanic eastern tropical Pacific (ETP) is defined as the area seaward of the continental shelf, from the Americas west to approximately 150° longitude, and from the U.S.-Mexico border south to central Peru. This area is roughly 21 million km^2, includes waters of 12 nations (Exclusive Economic Zones (EEZs) are shaded light gray) and the oceanic commons, and roughly corresponds to the area managed by two regional fishery management bodies: the Inter-American Tropical Tuna Commission (IATTC) and the Agreement on the International Dolphin Conservation Program (AIDCP). The area managed by the IATTC is outlined with a red hashed line; this is also the relevant area for AIDCP. The black segmented lines are ship tracklines from NOAA Fisheries surveys (1986–1990, 1998–2000, 2003, 2006). These surveys were conducted to assess populations of dolphins historically impacted by the tuna purse-seine fishery.

(**Figure 1**) and is relatively data rich compared to most other oceanic systems (Ballance et al., 2006 and references therein; Wade et al., 2007; Gerrodette et al., 2012).

Provisioning Services: Commercial Fisheries

The IATTC maintains an online source of publicly available data on commercial fisheries (defined here to exclude local, coastal fisheries) catches in the IATTC Convention area (**Figure 1**). These data are compiled from vessel logbooks, observer data, and a variety of other sources, and are considered the best scientific estimates of annual catch. Time series data range from 1918 through 2011, with data beginning in different years for different species groups. Retained catches (in mt, excludes discards for consistency) are aggregated by year, species group, vessel flag (country), and gear type. There are seven different gear types: purse-seine, longline, pole-and-line, troll, harpoon, gillnet, and hook-and-line. Using these data, we calculated: (1) annual catch by species group (listed below), with all gear types and vessel flags combined, (2) annual catch by vessel flag, with all species groups and gear types combined, and (3) percentage of total catch for each gear type, across all years, species groups, and vessel flags. We will refer to the fished species using their common names; Latin names are provided in **Table 1**.

The Office of Science and Technology of NOAA Fisheries maintains an online database of foreign trade fisheries statistics. For fish imported to the U.S., data on total weight imported (in kilograms) and price paid (USD) are aggregated by year, taxon (species group), product type, and export country. Data were available for 1975–2010 on U.S. imports from IATTC member countries (Colombia, Costa Rica, Ecuador, El Salvador, France, Guatemala, Japan, Mexico, Nicaragua, Panama, Peru, South Korea, Spain, Vanuatu, and Venezuela). We excluded countries located outside Latin America (France, Japan, South Korea, Spain, and Vanuatu) because the data include all fish imported from each country, regardless of where the fish were caught, and we wanted to focus exclusively on fish caught in the ETP (**Figure 1**). For Latin American countries belonging to both the IATTC and the International Commission for the Conservation of Atlantic Tunas (Mexico, Guatemala, Nicaragua, Panama, and Venezuela), we examined fishery profiles from the Food and Agriculture Organization of the United Nations to confirm that the large majority of fish are caught in the Pacific rather than the Atlantic (roughly 78–100% of each country's tuna purse-seiners operated in the Pacific). Thus, in order to use the U.S. imports data to calculate prices, we made the simplifying assumption that all fish imported from those countries were caught in the ETP; this assumption is benign if the U.S. import price for a product is the same regardless of whether the fish

TABLE 1 | Summary of commercial fisheries catches in the eastern tropical Pacific (ETP).

Species group	Data start	Cumulative catch	Mean catch	Sd. catch	Min. catch	Max. catch	Min. year	Max. year	2011 catch
Yellowfin tuna* (Thunnus albacares)	1919	12,656,133	136,087	109,585	136	439,317	1919	2002	202,762
Skipjack tuna* (Katsuwanus pelamis)	1918	7,657,572	81,464	75,650	499	298,323	1921	2008	279,007
Bigeye tuna* (Thunnus obesus)	1954	4,126,879	71,153	36,550	1,610	143,141	1954	2000	81,743
Albacore* (Thunnus alalunga)	1952	1,356,235	22,604	8727	123	45,390	2011	2003	123
Bonitos* (e.g., Sarda spp.)	1949	429,700	6931	5094	1	18,652	2002	1967	7958
Dolphinfishes* (Coryphaena spp.)	1971	283,613	6917	12,035	8	57,465	1972	2009	1718
Swordfish* (Xiphias gladius)	1945	448,808	6699	5673	504	21,340	2011	2010	504
Pac. bluefin tuna* (Thunnus orientalis)	1952	327,703	5462	3752	480	15,899	1991	1966	3187
Blue marlin (Makaira nigricans)	1954	245,669	4236	2061	212	12,043	2011	1963	212
Sharks, skates, rays* (Elasmobranchii)	1969	175,309	4174	4557	8	15,211	1969	2003	3098
Striped marlin (Kajikia audax)	1954	241,671	4,167	3248	16	14,213	1955	1968	36
Tunas nei* (Scombridae)	1970	155,623	3705	4135	225	18,195	1991	1998	1825
Black skipjack (Euthynnus lineatus)	1964	54,873	1247	1165	5	4359	1964	2009	2197
Indo-Pac. Sailfish (Istiophorus platypterus)	1975	32,648	882	589	6	2291	1990	1993	20
Unidentified fishes (Oste- & Chondr- ichthyes)	1961	38,353	834	984	6	4956	1970	2003	684
Marlins, sailfishes, & spearfishes nei (Istiophoridae)	1967	18,120	421	594	0	1948	1976 1980	2001	21
Black marlin (Istiompax indica)	1954	18,187	314	215	13	905	1954	1973	52
Carangids nei (Carangidae)	1959	10,172	199	251	10	1240	1970	1983	79
Shortbill spearfish (Tetrapturus angustirostris)	1986	4,377	182	145	0	519	1989	2010	NA
All Species Groups	1918	28,281,645	300,869	245,136	1089	906,250	1921	2003	585,226

"Data start" is the year in which data collection began for each species group. "Cumulative catch" sums annual catch values (in mt) from the "Data start" year through 2011. All other catch values are in mt per year. "Mean catch," "Sd. Catch," "Min. catch," and "Max. catch" are the mean, standard deviation, minimum, and maximum of annual catches. "Min. year" and "Max. year" are the years with the minimum and maximum annual catches. "*" denotes species groups with the 10 highest maximum annual catch values; those groups are included in **Figure 3**. "spp." indicates multiple species within a taxonomic group. "nei" means "not elsewhere included"—meaning, the fish were not assigned to a particular species group (e.g., "tunas nei" includes all tunas not identified to species). Data source: Inter-American Tropical Tuna Commission (IATTC) public data.

were caught in the Atlantic or the Pacific. We focused on the top 10 species groups in terms of maximum annual catch (from the IATTC dataset, **Table 1**). Those species groups were as follows, with a breakdown of product types by total weight imported for each: (1) yellowfin tuna—83% whole fresh/frozen, 14% fresh, 3% eviscerated/prepared fresh/frozen, (2) skipjack tuna—100% fresh/frozen, (3) bigeye tuna—99% fresh, 1% frozen, (4) albacore tuna—69% canned, 31% fresh/frozen, (5) bonitos—100% canned, (6) dolphinfish—89% frozen filets, 11% fresh, (7) swordfish—94% fresh/frozen, 6% prepared fresh/frozen meats, (8) Pacific bluefin tuna—100% fresh/frozen, (9) sharks/rays—91% fresh/frozen, 9% dried/oil, and (10) tunas other—62% canned, 38% other prepared/frozen meats.

For each species group, we calculated an average price per mt for each year (1975–2010). Though ex-vessel fish prices (i.e., prices paid to vessels for landings) would be the ideal prices to use, because these were not available, we used the U.S. import prices, which add value to ex-vessel prices to the extent the fish are processed and transported. This approach provided a U.S.-centric view; however, such time series data are unique and to our knowledge, these were the best available data for this system (see Discussion for further caveats). Applying the calculated average prices to total annual catches, we estimated the total U.S. import price value ("catch value") for each species group for all years. Total catch values were adjusted for inflation using the online

U.S. Inflation Calculator, which is based on U.S. government consumer price index data. All values are presented in 2010 USD, allowing for comparisons across years. For each species group, and for all 10 species groups combined, we summarized annual catch and catch value, and investigated trends using linear regressions and LOESS smoothed regressions (Cleveland and Devlin, 1988). We examined trends in catch value pre- and post-1990. This break corresponds to the introduction of the U.S. "dolphin-safe" label, which was created in response to historically high mortality of dolphins in the ETP purse-seine fishery (Wade et al., 2007). The mortality was caused by the common method of chasing and encircling dolphins in order to capture large tunas swimming below them (Wade et al., 2007). The "dolphin-safe" label signals to consumers that dolphins were not set upon during the fishing trip that produced the tuna (Wade et al., 2007).

Focusing on the purse-seine fishery for yellowfin tuna (the gear type and species, respectively, with the highest cumulative catch for 1918–2011), we mapped in a spatially-explicit way cumulative effort and catch for a 20 year period (1986–2006). Effort was measured as the number of purse-seine sets on 3 different targets (dolphin schools, floating objects, and schools of tuna unassociated with objects or dolphins); catch was measured as mt of fish retained. These data were provided by IATTC through a special agreement. The spatial resolution was 2° latitude by 2° longitude for most of the data. When effort in a

grid cell represented fewer than 3 vessels or was solely within one country's Exclusive Economic Zone (EEZ), the data were provided at a resolution of 5° to maintain confidentiality. For 5° by 5° cells, we divided catch and effort by 6.25 (the number of 2° by 2° cells in one 5° by 5° cell) to standardize values to the 2° by 2° cells. We binned the catch and effort data into 5 quantitative categories for mapping purposes.

Data on the port-specific geographical distribution of purse-seine fishery landings in 2010–2011 were provided by IATTC for this study. Species groups included yellowfin, skipjack, bigeye, albacore, black skipjack, bullet, frigate, and Pacific bluefin tunas, eastern Pacific bonito, striped bonito, dolphinfishes, and tunas not elsewhere included (i.e., tunas that were not assigned to the above species groups). We mapped the 2010–2011 mean annual percent of total landings for each port. For each country, the data also included the percentage of landings brought to shore by vessels carrying the flag of that country. From this, we determined the proportion of landings in each country that was supplied by foreign vessels.

Regulating Services: Carbon Storage

This service, in principle, involves three main processes: (i) the geophysical transport of atmospheric CO_2 into the ocean (a flow, in economic terms), (ii) the biological transport of carbon (C) from the surface layer to deep ocean sediments (also a flow), and (iii) the storage of C in populations of marine animals (multiple stocks). Our approach to investigating these processes and their associated values was as follows. First, we ignored geophysical transport because it is not directly affected by human activities in the ocean (i.e., there are no trade-offs between alternative management policies) and focused instead on the latter two, which can be affected by human uses of ocean resources (e.g., commercial fishing). Second, for biological transport, we estimated the quantity and value of the flow for the entire ETP; however, because the impacts of humans on this service are complex and poorly understood, we did not attempt to estimate any changes in C associated with human activities. It is worth noting that if human activities have decreased the amount of carbon exported annually, our calculations here likely underestimate the true potential value of the biological pump. Third, to provide examples of carbon values that are impacted by human uses in a more identifiable way, we investigated: (i) the reduction in the *stock* of C in fish populations exploited by the ETP purse-seine fishery and (ii) the reduction in the *stock* of C in dolphin populations as a result of historical bycatch in the same fishery. For any population, the best estimate of a fisheries-induced reduction in standing stock biomass is the difference between the biological carrying capacity (the equilibrium biomass that would be achieved without fishing) and the standing stock biomass at the current harvest level (with the assumption that the harvest level would continue in perpetuity). While we had data to calculate this difference for the dolphin populations, we did not have data to do so for the multiple targeted fish species. Therefore, we examined annual fishery biomass removals (a flow) as a first-order approximation of the reduction in the biomass of the fish stocks as a result of fishing. Management policies to rebuild fisheries-depleted stocks

of dolphins or fish would include additional benefits of increasing carbon storage and its value by the amounts estimated here.

We estimated the amount of C biologically exported annually from the surface to the deep ocean in the ETP, and the potential market value of this carbon. Emerson et al. (1997) estimated that 24 g of C m^{-2} yr^{-1} are exported from the surface to the deep ocean in an oligotrophic (nutrient poor) area in the Pacific Ocean. Portions of the ETP, notably, the Equatorial Cold Tongue and the Costa Rica Dome, are characterized by high nutrient concentrations relative to oligotrophic waters (Fiedler and Talley, 2006), suggesting export is higher in the ETP. Indeed, mean export for the region has been modeled as 38 g C m^{-2} yr^{-1} (Schlitzer, 2004). However, we used 24 g C m^{-2} yr^{-1} as a conservative estimate for our calculations. We multiplied this value by 2.1×10^{13} m^2 (the estimated surface of the ETP study area) to estimate the amount of C exported annually. We converted this value to number of CO_2 trading units (1 trading unit = 1 mt of CO_2 = 0.2729 mt of C + 0.7271 mt of O_2). To estimate the potential market value of this C, we used a range of prices from the European Union Allowances Emissions Trading System, the largest carbon market in the world in 2014 (World Bank, 2014). We used an average 2013 price of $7 mt^{-1} (with $5 and $9 as lower and upper limits) to estimate potential value for that year (USIWG, 2013; World Bank, 2014). For a potential future scenario, we used $35 mt^{-1}, an estimate of the price required to achieve climate stabilization goals and pay for climate-change related damages (USIWG, 2013; World Bank, 2014). This price was also observed in 2008 before the major economic downturn (Capoor and Ambrosi, 2009; Newell et al., 2013, 2014).

The tuna purse-seine fishery has impacted the amount of carbon stored in populations of large vertebrates, specifically populations of fish that are targeted directly or indirectly affected through bycatch (Gerrodette et al., 2012) and populations of dolphins that were historically depleted through incidental mortality (Wade et al., 2007). For the fish populations, we estimated the amount of C that is removed annually by applying a total body carbon content of 11.5% (Czamanski et al., 2011) to the annual purse-seine fishery biomass removals of 543,533 mt (Gerrodette et al., 2012). As noted above, we used the annual biomass removals here to provide an order-of-magnitude estimate of the reduction in standing stock biomass for the fished populations, as we do not know the true extent to which fishing has reduced the various fish stocks. After converting from mt of C to equivalent CO_2 trading units, we applied the same range of market prices as above. For the depleted dolphin populations, we calculated the difference between the estimated pre-exploitation population size for 1958 (Wade et al., 2007) and the most recent population estimate for 2006 (Gerrodette et al., 2008). Between 1958 and 2006, the population of northeastern offshore spotted dolphins decreased by 76% from 3.6 million individuals (Wade et al., 2007) to 857,884 individuals (Gerrodette et al., 2008). The eastern spinner dolphin population decreased by 41% from 1.8 million individuals (Wade et al., 2007) to 1,062,879 individuals (Gerrodette et al., 2008). To calculate lost standing stock biomass (mt), we multiplied those differences in population size by a mean body mass of 65.4 kg and 52.5 kg for northeastern offshore

spotted and eastern spinner dolphins, respectively (Trites and Pauly, 1998; Perrin et al., 2005). We applied a total body carbon content of 25% (based on an estimate for humans by Wang and Pierson, 2010 as a mammalian approximation) to that biomass, converted it to equivalent CO_2 trading units, and applied a market price of CO_2 to estimate the potential market value of the lost carbon.

Cultural Services: Recreational Fishing

The Billfish Foundation (TBF) exists to promote the conservation of billfish (marlins, sailfish, and swordfish) and associated species (e.g., tunas), healthy oceans, and a sustainable recreational fishing industry that targets these species. TBF lobbies for conservation-based management of both commercial fisheries and recreational fisheries as part of its strategy. Recently, TBF released a series of sport fishing socio-economic studies for three locations in Latin America: Los Cabos (Baja California Sur, Mexico), Costa Rica, and Panama (Southwick et al., 2008, 2013; Jimenez et al., 2010). The purpose of those studies was to demonstrate the economic value of sport fishing to local economies. This effort, which included surveys of tourists at airports, anglers, hotels, restaurants, and local businesses, appears to be the first major attempt to quantify the economic impact of sport fishing in Latin America. The reports also aim to understand the factors appealing to international anglers traveling to those locations (mostly from the U.S.). We believe these reports, with their focus on highly migratory pelagic species, contain uniquely relevant information for understanding different uses of ETP ES. We assume they represent areas with high (if not the highest) levels of sport fishing in the ETP. We note that the sequence of the studies (Los Cabos, Costa Rica, Panama) may mimic the progression of development in the industry from north to south. Focusing solely on fishing trip expenditures as direct economic impacts (e.g., retail sales including charter boats, lodging, food, transportation, tackle, etc.) and excluding indirect or induced economic impacts (e.g., jobs, taxes, multipliers, etc.), we summarized the important findings across the three reports as an example of key cultural services provided by this region. Due to the limited geographic scope of these data, the summarized expenditures provide only a minimum estimate (an underestimate) of total expenditures in the region. We did not attempt to scale these numbers up or apply them to other sport fishing locations in the region, as we lacked sufficient data (e.g., number of charter vessels, trips, visitors, hotels, etc.) to do so.

Supporting Services: Biodiversity/Density

The Southwest Fisheries Science Center (NOAA Fisheries) conducted extensive vessel-based surveys of the ETP between July and December in 1986–1990, 1998–2000, 2003, and 2006. Most effort occurred between August and November. Trained biologists collected data on cetaceans (whales, dolphins, and porpoises), seabirds, marine turtles, and ichthyoplankton (includes larval fishes, squids, and octopuses), including the species, number of individuals, and location of all observed or collected animals. Cetacean data were col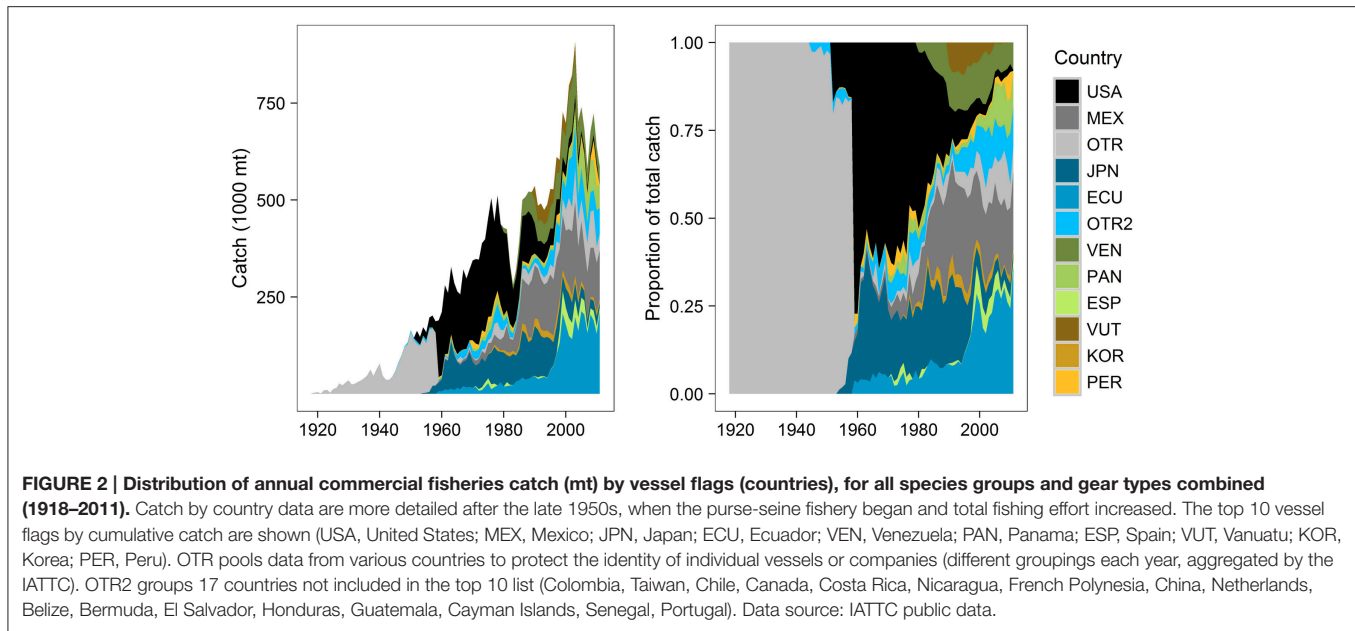lected using standard visual line-transect survey methods (Gerrodette and Forcada, 2005) in all 10 survey years. Ichthyoplankton samples were collected daily using manta net tows (Vilchis et al., 2009) from 1987 onward. Seabird data were collected using standard visual strip-transect survey methods (Ballance, 2007) starting in 1988. Marine turtle data were collected during the cetacean line-transect surveys from 1998 onward.

To investigate biodiversity patterns for cetaceans, seabirds, and ichthyoplankton, we calculated species richness (the total number of species observed during all years combined) using a spatial resolution of 2° by 2°. Sightings or specimens identified to order, family, or genus only counted toward the species tally if a species within that higher taxon had not already been observed in that cell. We used the same spatial grid for turtles, but we calculated sightings density rather than species richness because nearly all sightings were of a single species, olive ridley (*Lepidochelys olivacea*). Survey effort (the number of search hours for cetaceans, seabirds, and turtles, and total volume of water filtered by net tows for ichthyoplankton) was also calculated per grid cell. Our calculations were limited to the four taxa for which we had spatially explicit long-term survey data, making them conservative (minimum) estimates for the entire ETP ecosystem. To provide conservation context for cetaceans, seabirds, and marine turtles, we compared the total number of species that occur in the ETP to the global number of species for each taxon, and we determined the conservation status for those species using the Red List of Threatened Species of the International Union for the Conservation of Nature (IUCN, 2012). For marine turtles, the number of species was derived from IUCN distribution maps.

RESULTS

Commercial Fisheries

Commercial fisheries operating in the ETP from 1918 to 2011 caught an estimated total of 28,281,645 mt (**Table 1**). Of this cumulative catch, 65% was captured using purse-seines, 18% by longlines, 9% with pole-and-line methods, and the remaining 8% with trolls, harpoons, gillnets, and hook-and-line methods. In 2011, purse-seines accounted for 95% of total catch. Annual catch ranged from 1089 to 906,250 mt (mean = 300,869 mt, CV = 82%) across all years, with an increasing trend over time and high values in recent years that are often double the mean (e.g., 585,226 mt in 2011; **Table 1**, **Figures 2**, **3**). For 1975–1990, mean annual catch was 433,811 mt (range: 268,796–524,849 mt, CV = 17%); for 1991–2010 it was 632,596 mt (range: 459,078–891,019 mt, CV = 19%); and for 1975-2010 it was 544,247 mt (range: 268,796–891,019 mt, CV = 27%). Yellowfin tuna was by far the top species in terms of cumulative catch over time, mean annual catch, and maximum annual catch (**Table 1**). It also had the largest range of annual catch amounts, with a minimum of 136 mt in 1919 and a maximum of 439,317 mt in 2002. Skipjack tuna had the next highest cumulative catch and mean annual catch, both of which were roughly 60% of those amounts for yellowfin tuna. In 2011, the skipjack catch exceeded that of all other species. Bigeye tuna was the third most important species, with cumulative and mean annual catches 33 and 52% of the

FIGURE 2 | Distribution of annual commercial fisheries catch (mt) by vessel flags (countries), for all species groups and gear types combined (1918–2011). Catch by country data are more detailed after the late 1950s, when the purse-seine fishery began and total fishing effort increased. The top 10 vessel flags by cumulative catch are shown (USA, United States; MEX, Mexico; JPN, Japan; ECU, Ecuador; VEN, Venezuela; PAN, Panama; ESP, Spain; VUT, Vanuatu; KOR, Korea; PER, Peru). OTR pools data from various countries to protect the identity of individual vessels or companies (different groupings each year, aggregated by the IATTC). OTR2 groups 17 countries not included in the top 10 list (Colombia, Taiwan, Chile, Canada, Costa Rica, Nicaragua, French Polynesia, China, Netherlands, Belize, Bermuda, El Salvador, Honduras, Guatemala, Cayman Islands, Senegal, Portugal). Data source: IATTC public data.

yellowfin tuna amounts. Catch data for skipjack and yellowfin tuna date to 1918–1919, while data for bigeye tuna only date back to 1954. Together, these 3 species comprise 86% of the cumulative catch.

Understanding stakeholders (who they are and their degree of investment) is an important component of EBM. Twenty-seven countries fished (legally, based on IATTC data) in the ETP from 1918 to 2011, each with a unique trend in annual catch (**Figure 2**). Countries with the highest percentage of cumulative catch across all years included the U.S. (23%), Mexico (14%), Japan (13%), Ecuador (13%), Venezuela (6%), and Panama (4%). U.S. catch increased notably from the 1950s (**Figure 2A**), peaked in the late 1970s when the U.S. captured 60% of the total catch (**Figure 2B**), and tapered to nearly zero in 2011. Mexico's catch gradually increased from the 1960s to the 1980s and remained relatively stable thereafter (**Figure 2A**); it was 22% of total catch in 2011 (**Figure 2B**). Japan's catch was fairly consistent from the late 1950s through the early 1990s (**Figure 2A**), but decreased in the 2000s and only represented 2% of the total in 2011 (**Figure 2B**). Ecuador's catch slowly increased from the 1960s onward (**Figure 2A**); in 2011, it captured the largest portion of total catch (37%) (**Figure 2B**). Venezuela began fishing in the early 1980s, increased its catch into the 1990s (**Figure 2A**), and acquired an 8% share of total catch in 2011 (**Figure 2B**). Panama's relatively small fleet appeared in the 1970s, grew in the 2000s (**Figure 2A**), and claimed 10% of total catch in 2011 (**Figure 2B**). Colombia is represented in the "Other" categories in **Figure 2** because it only caught 1% of the cumulative catch; however, in 2011, its portion of total catch was 8%. Spain, Vanuatu, Korea, Peru, Taiwan, and Chile each caught 1–2% of the cumulative total. Spain, Korea, Nicaragua, and Taiwan each caught 1–2% of the 2011 total.

Increases ($p < 0.01$) occurred in both annual catch and catch value from 1975 to 2010 for yellowfin, albacore, dolphinfish, swordfish, and the "all species" group (**Figure 3**). Increases

in catch and catch value were notably disproportionate for yellowfin tuna (only a 30% increase in mean annual catch, but a 239% increase in mean annual catch value after 1990), and for "all species" (46% increase in catch and 226% increase in catch value after 1990). There was a significant increase ($p < 0.001$) in the mean annual price for yellowfin tuna over time, which was $2222 mt^{-1} for 1975–1990 and $5492 mt^{-1} for 1991–2010. For "all species," mean annual price was $3111 mt^{-1} across all years (range: $1431–$6339 mt^{-1}, CV = 53%), but increased from $1932 mt^{-1} for 1975–1990 to $4055 mt^{-1} for 1991–2010. Mean annual catch value increased from $830 million for 1975–1990 to $2.7 billion for 1991–2010, and was $1.9 billion for the entire period (range: $487 million–$4.7 billion, CV = 76%). Trends for "all species" largely reflect trends for yellowfin tuna, as it comprises 46% of the cumulative catch in this period (**Figure 3**).

Trends in annual catch and catch value for the remaining species groups varied. Bonitos were the only group with significant decreases ($p < 0.01$) in both annual catch and catch value (**Figure 3**). There was no significant trend in catch for bluefin tuna, but value significantly increased ($p < 0.001$) (**Figure 3**) due to an increase ($p < 0.10$) in the price (mean of $5424 mt^{-1} for 1989–1990 and $10,853 mt^{-1} for 1991–2010). For skipjack, bigeye, and elasmobranchs, annual catch increased significantly ($p < 0.001$), but there was no significant trend in value (**Figure 3**), due to significant decreases ($p < 0.01$) in the price for skipjack tuna (mean of $1836 mt^{-1} for 1975–1990 and $1355 mt^{-1} for 1991–2010) and elasmobranchs (mean of $33,026 mt^{-1} for 1975–1990 and $3820 mt^{-1} for 1991–2010). The price for bigeye tuna did significantly increase ($p < 0.01$), but a decreasing trend in catch over the years for which we had price data (2001–2010) probably canceled this effect, leading to the absence of significant change in the total catch value. There were no significant trends for the "tunas—other" group.
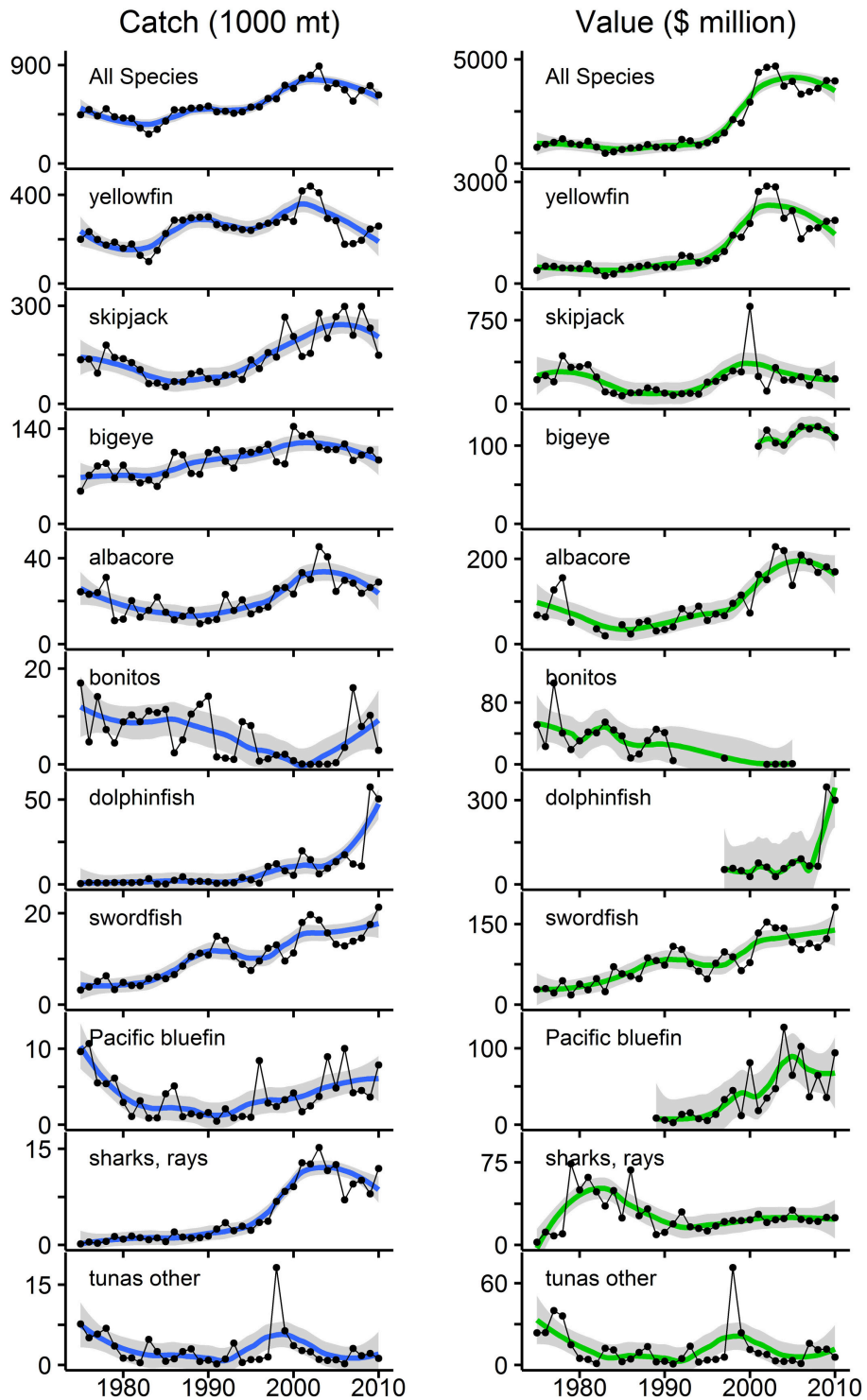
FIGURE 3 | Annual catch and estimated catch value (using U.S. import prices) for the top 10 commercially fished species groups in the eastern tropical Pacific (ETP) for 1975–2010. These 10 groups rank highest in terms of maximum annual catch (**Table 1**). "Tunas other" corresponds to "tunas nei" from **Table 1** and represents all tunas not assigned to individual species groups. All gear types and fishing nations are represented. Left panels are annual catch in mt; right panels are estimated catch value in millions of 2010 U.S. dollars (adjusted for inflation). Note: the scales for catch and value vary by species group. Data points are connected with lines for sequential years; breaks appear where no data were available. LOESS smoothed trend lines are displayed with shaded 95% confidence intervals. The top panel is the sum of the 10 species groups. Over 35 years, cumulative catch and catch value were 19.6 million mt and $67.4 billion, respectively. Mean annual catch was 544,247 mt (range: 268,796–891,019 mt; sd: 144,698 mt). Mean annual catch value was $1.9 billion (range: $487 million–$4.7 billion; sd: $1.4 billion) for the entire period. Data sources: IATTC public data and NOAA Fisheries public data.

Analysis of catch and price trends indicated ordinary demand-supply dynamics, with various scenarios apparent across the species groups. Note that the following results may only reflect the U.S. market for imports and not necessarily markets in Latin America or Europe. First, an *increasing supply of fish* was accompanied by: (i) a *decreasing price* for skipjack and elasmobranchs, indicating that supply was increasing at a higher rate than demand, (ii) an *increasing price* for yellowfin, bigeye, albacore, and dolphinfish, indicating that demand was increasing at a higher rate than supply, and (iii) *no change in price* for swordfish and all species combined, suggesting that either (a) demand was increasing at the same rate as supply, maintaining a constant equilibrium price, or (b) long-run demand was perfectly elastic and thus equilibrium price was unaffected by changes in supply. Second, a *decreasing supply of fish* only occurred for bonitos, and was associated with *no change in price*, indicating either (a) demand was decreasing at the same rate as supply, or (b) long-run demand was perfectly elastic. Finally, an *unchanging supply of fish* was associated with: (i) an *increasing price* for bluefin, suggesting an increasing demand, and (ii) *no change in price* for "tunas—other," indicating no change in demand.

Spatial patterns for purse-seine fishery effort and yellowfin tuna catch were slightly different (**Figure 4**). The highest concentrations of catch occurred between the southern tip of Baja California and Mazatlan, near the Costa Rica Dome (near 90°W, 9°N), and along thermocline ridge. Concentrations of effort were also highest in those regions but had a broader geographic extent and a clearer gradient of high values in the east and low values in the west.

ETP purse-seine fishery landings in 2010–2011 were distributed across ports in the following countries (**Figure 4B**): Ecuador (51%), Mexico (25%), Colombia (9%), El Salvador (5%), Guatemala (3%), Costa Rica (3%), Venezuela (3%), and Peru (2%). Differences between 2010 and 2011 percentages were 0–2% for all port locations except Manta, Ecuador, where the percentage of total landings increased from 36 to 44%. The 2010-2011 mean percentages of landings that were brought to shore by vessels with the port's national flag were: Venezuela (100%), U.S. (100%), Mexico (96%), Colombia (75%), El Salvador (68%), Ecuador (62%), Guatemala (6%), Costa Rica (0%), and Peru (0%). In reverse order, this ranked list indicates the importance of foreign vessels in landing fish in these ports (i.e., landings in Peru were all from foreign vessels, whereas landings in Venezuela were all from domestic vessels). These percentages for each country varied 0–6% between years, with the exception of a 14% decrease for Ecuador (i.e., a higher percentage of landings by foreign vessels in 2011). For the U.S., there were only data for 2011.

Carbon Storage

Our conservative estimate for the amount of C exported from the surface to the deep ocean in the ETP was 5.0×10^{14} g or 5.0×10^8 mt of C yr^{-1}. This was equivalent to 1.8×10^9 trading units of CO_2, which had a total carbon value of \$12.9 billion yr^{-1} (range: \$9.2–\$16.6 billion yr^{-1}). At the highest carbon price of \$35 mt^{-1}, the ETP's export service would be worth \$64.7 billion yr^{-1}.

The 2.74 million northeastern offshore spotted dolphins lost from the population represented a total biomass of 179,334 mt, of which roughly 44,834 mt was C. This C amount was equivalent to 164,286 mt of CO_2 trading units, with a cumulative (not annual) total value of \$1,398,161 (range: \$998,687–\$1,797,636). Spreading this value across the 2.74 million dolphins yields a potential carbon storage value per dolphin of \$0.42 (range: \$0.30–\$0.54). At a carbon price of \$35 mt^{-1}, the value of the lost portion of the population would be \$5,750,003, or \$2.10 per dolphin.

The reduction of the eastern spinner dolphin population by 737,121 individuals represented a loss of 38,699 mt total and 9675 mt of C from the system. This was equivalent to 35,451 mt of CO_2 trading units worth a cumulative total of \$248,160 (range: \$177,257–\$319,063) or \$0.34 per dolphin (range: \$0.24–\$0.43). The value would be \$1,240,802, or \$1.68 per dolphin, if the carbon price were \$35 mt^{-1}.

FIGURE 4 | (A) Commercial purse-seine fishery effort as the cumulative number of sets from 1986 through 2006. **(B)** Yellowfin tuna catch (cumulative mt) in the purse-seine fishery over the same period. Proportional circles depict the percentage of annual purse-seine landings (all species) brought to different ports in 2010–2011. Landings were distributed as follows, with numbers corresponding to map locations: (1) Ensenada, Mexico (1%); (2) Mazatlan, Mexico (14%); (3) Manzanillo, Mexico (6%); (4) Puerto Chiapas, Mexico (4%); (5) Puerto Quetzal, Guatemala (3%); (6) La Union, El Salvador (5%); (7) Puntarenas, Costa Rica (3%); (8) Cartagena, Colombia (7%); (9) Barranquilla, Colombia (2%); (10) Puerto Sucre, Venezuela (3%); (11) Manta, Ecuador (40%); (12) Posorja, Ecuador (11%); (13) Paita, Peru (2%).