Productivity and Biomass of Fishes in the California Current Large Marine Ecosystem:
Comparison of Fishery-Dependent and -Independent Time Series

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13 ABSTRACT

14 Commercial landings are often the only data available to assess the status of marine fish
15 populations, but may reflect economics, technology and management policy in addition to stock
16 size. In the California Current Large Marine Ecosystem (CCLME), the availability of CalCOFI
17 ichthyoplankton data enabled us to compare commercial landings with a fishery-independent
18 time series from 1951 to 2011. Fishery landings for the CCLME generally increased over this
19 period, peaking about 1990 and displaying no clear subsequent trend. However, the abundance of
20 ichthyoplankton in the southern CCLME has declined by ~70% since about 1970, based on the
21 decline of taxa with cool-water affinities, apparently related to ocean warming and reduced
22 productivity, and of mesopelagic taxa since the 1990s in response to declining midwater oxygen
23 concentrations. These results highlight the importance of sustained fishery-independent time
24 series at a time of secular climate change.

25 Calibration of the larval fish abundance time series with stock assessments and
26 acoustic/trawl surveys provided a proxy time series of spawning stock biomass for epi- and
27 mesopelagic planktivores since 1951. We estimate that mesopelagic fishes comprised ~83% of
28 the biomass of plankton-feeding fishes in the southern CCLME, but their prey consumption
29 appears approximately equivalent to that of epipelagic planktivores because of the greater
30 metabolic requirements of epipelagic fishes. The “wasp-waist” paradigm for eastern boundary
31 currents needs to be re-assessed based on revised assessments for the abundance of mesopelagic
32 fishes.

33 Keywords: Climate, fishery yield, California Current, fishery-independent time series,
34 mesopelagic fishes, planktivores

35

INTRODUCTION

Studies of the effects of climate on marine fish generally focus on commercial fisheries, in part because of the socioeconomic importance of fisheries but also because commercial fishery statistics and stock assessments often provide the only time series available for marine fishes. However, it is estimated that >80% of global fish landings are from fisheries that lack formal stock assessments (Costello et al. 2012). As a result, studies often rely on the fishery itself and, in particular, on the record of commercial landings, as their primary source of data (e.g. Myers and Worm 2003, Teixeira and Cabral 2009). However, it is well known that such data are subject to a variety of biases, such as misreporting, the effects of market conditions, changing technology, and fishery regulations. Even where fishery-independent data are available, they may pertain only to a relatively few commercial species. This bias toward commercial fisheries is also unfortunate in that it greatly limits the scope of oceanographic investigations. Fishes are by far the most diverse vertebrates on the planet, filling a great variety of ecological niches, but only a small fraction of fish taxa are subject to significant fisheries. Indeed, noncommercial taxa appear to dominate the fish biomass over most of the world's oceans (Irigoien et al. 2014, Davison et al. 2015).

In the California Current Large Marine Ecosystem (CCLME), it is possible to examine the implications of relying on commercial landings data and to go beyond such data to examine how the region's broader fish communities are responding to climate and other potential drivers. Ichthyoplankton surveys have been carried out as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program since 1951, with surveys conducted mostly on a monthly-to-quarterly basis. All larval fish are removed, identified and enumerated from oblique net tows to ~210 m depth at a grid of stations that consistently covers southern and central California (Fig. 1). Most marine fishes are broadcast spawners and inhabit the upper 200 m during their early life history so plankton collections can quantitatively sample most of a region's fish community, including mesopelagic taxa, as eggs and larvae. Because the larvae in these collections are predominantly at a preflexion early stage, their abundance provides an index of spawning stock biomass, as demonstrated for a number of key species in the CCLME, such as Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), various rockfishes (*Sebastes* spp.), and California halibut (*Paralichthys californicus*) (Moser and Watson 1990, Moser et al. 2000, 2001, Koslow et al. 2011).

Recent studies based on the CalCOFI ichthyoplankton and other fishery-independent time series have described dramatic patterns of decline across broad segments of the fish communities in the southern CCLME. Some 24 taxa across 8 families of mesopelagic fishes have declined by approximately 60% since the 1990s, highly correlated with declining midwater oxygen concentrations and a concomitant expansion of the oxygen minimum zone (OMZ) (Bograd et al. 2008, McClatchie et al. 2010, Koslow et al. 2011). Nearshore fishes quantitatively sampled since 1972 from the cooling water intakes of southern California power plants have declined >70%, related to a northward shift in the community composition (Miller and McGowan 2013). This trend is highly correlated with an ~70% decline in the overall abundance of larval fishes in the CalCOFI time series, due to a decline of taxa with cool-water affinities, including several of the most abundant taxa in the time series (e.g. northern anchovy, Pacific hake, rockfishes, northern lampfish (*Stenobranchius leucopsarus*) and California smoothtongue (*Leuroglossus stilbius*) (Koslow et al. 2013, submitted).

80 The availability of fishery-independent time series enables us to compare trends in stock
81 biomass with commercial fishery landings, as well as to compare trends in the broader fish
82 community with trends in the region's fisheries. The CCLME has been upheld as an example of
83 a region that has successfully rebuilt its exploited fish populations (Worm et al. 2009). However,
84 that study did not make use of the CalCOFI or other ichthyoplankton time series to assess the
85 status of regional fish communities, relying instead largely on stock assessments for
86 commercially exploited species. Are the patterns from the CalCOFI fishery-independent larval
87 time series consistent with the Worm et al. (2009) assessment?

88 In the southern CCLME, it is also possible to combine data on long-term relative
89 abundance from the CalCOFI ichthyoplankton time series with data on stock biomass from
90 periodic stock assessments for commercially-exploited species that spawn in the CalCOFI survey
91 area and from quantitative acoustic and trawl surveys that targeted ecologically important groups
92 such as mesopelagic fishes that are not commercially exploited (Davison et al. 2013, 2015).
93 Using the ichthyoplankton time series as a proxy should thus enable us to examine long-term
94 changes in the status of fish communities in the CCLME. We will focus in particular on the epi-
95 and mesopelagic planktivores: their relative importance as zooplankton consumers and as forage
96 for higher trophic levels, and how their relative roles have potentially shifted since the mid-
97 twentieth century.

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METHODS

Data sources

Commercial fishery landings data for the CCLME were obtained from the record of US commercial fishery landings for the states of California, Oregon and Washington available from NOAA (2015). We also obtained data from the Sea Around Us Project at the University of British Columbia, which sources its data primarily from the Food and Agriculture Organization of the United Nations. The main trends in these two data sets were similar, and only the NOAA data are shown. All major finfish fisheries and market squid (at times the dominant pelagic fishery in California) were included. CalCOFI ichthyoplankton data were obtained from the NOAA CalCOFI web-site and were processed as detailed in Koslow et al. (2011, 2013) except with regard to the stations included and the current use of resampling interpolated larval density to reduce spatial bias in the occupation of CalCOFI stations. Annual means were calculated from the seasonal means for the abundance of larvae (ind. 10m^{-2}) in the extended study area (Fig. 1). The time series since 1984 is based primarily on seasonal (quarterly) rather than monthly surveys, so analysis of monthly variability (e.g. to assess phenological variability) is not possible. Estimates of mesopelagic biomass were based on midwater trawl and acoustic survey data obtained during CalCOFI cruises from 2010-2012 (Davison et al. 2015) and trawl data from cruises in 2008-2009 that extended over much of the CCLME from the CalCOFI survey area to the waters off northern California, Oregon and Washington (Davison et al. 2013). Our classification of mesopelagic fishes as vertically migratory or not follows Table 2 in Davison et al. (2015).

Data analysis

Time series for the biomass of key groups were estimated by combining the ichthyoplankton data, which provide relative indices of spawning stock biomass since 1951, with formal stock assessment or acoustic/trawl survey estimates of spawning stock size, which calibrated or pegged the absolute spawning stock for a period of years. Thus, a linear regression between the ichthyoplankton abundance and absolute biomass estimate, if significant, provided a linear relationship between the two that allowed spawning stock biomass to be estimated from larval abundance for years without stock biomass estimates. The time series were tested first for normality and homoscedasticity. Time series that failed these tests were log-transformed, which rectified the problem. Acoustic/trawl estimates for mesopelagic fishes in the CCLME were obtained from Davison et al. (2013, 2015) for CalCOFI and other cruises between 2008 and 2012. Following Davison et al. (2015), mean trawl biomass in the CalCOFI area (2008-2012) was 4.2 g m^{-2} , and a trawl capture efficiency of 14% was assumed (Koslow et al. 1997, Davison et al. 2015). The study area over which mesopelagic biomass was estimated for comparison with the biomass of small epipelagic planktivores was the area from San Diego to San Francisco (CalCOFI lines 60 to 93.3) (Fig. 1), the approximate spawning area of the Pacific sardine (Smith 2005), equivalent to 8° latitude and extending from the coast to $\sim 300\text{ km}$ offshore (total area: $263,300\text{ km}^2$). The ratio of the mean mesopelagic fish biomass and mean mesopelagic ichthyoplankton abundance from 2008-2011 was applied to the CalCOFI ichthyoplankton time series (1951-2011) to obtain our time series for mesopelagic fish biomass. The biomass of mesopelagic vertical migrators relative to non-migratory fishes was based on the known migratory behavior of mesopelagic fishes in the CCLME summarized in Davison et al. (2015, Table 2) and their mean biomass from the trawl samples that sampled the water column from the

surface to 500 m depth. Jack mackerel (*Trachurus symmetricus*) biomass was estimated from NOAA acoustic/trawl surveys of 2006, 2008, and 2010 (Zwolinsky et al. 2012). Stock assessments for northern anchovy (Methot 1989), Pacific sardine (Hill et al. 2012), and Pacific mackerel (*Scomber japonicus*) (Crone et al. 2009, 2011) were used for their spawning stock biomass estimates.

Plankton consumption by major group was estimated based on that group's spawning stock biomass multiplied by that group's estimated ration (R) derived from the standard equation: $aR = M + G$, where a is the assimilation efficiency, assumed here to be a constant (0.8), M is the active metabolic rate, and G is the rate of growth and reproduction. The values for ($M + G$) in $\text{kcal yr}^{-1} \text{g}^{-1}$ wet weight over a year were obtained from Childress et al. (1980, Table 1): 13.3 $\text{kcal yr}^{-1} \text{g}^{-1}$ wet weight for Pacific sardine based on Lasker (1970), which was assumed to be representative of epipelagic planktivores, and 4.1 and 0.96 $\text{kcal yr}^{-1} \text{g}^{-1}$ wet weight, the mean value for migratory and non-migratory midwater fishes, respectively. The energy density of their prey was assumed to be 1 kcal g^{-1} wet weight (Clark and Prince 1980).

RESULTS

The time series of commercial fishery landings from the CCLME (1950- 2013) indicates that overall landings have tended to increase over time: from 100-200 thousand tonnes in the 1950s and 1960s to about 150 to 250 thousand tonnes in the 1970s to early 1990s to about 250 to 350 thousand tonnes since the early 1990s (Figure 2). However, landings for individual taxa generally varied considerably over this period: Pacific sardine dominated landings during the 1950s, northern anchovy in the 1970s, rockfishes in the 1980s, and Pacific hake (*Merluccius productus*), Pacific sardine and market squid (*Doryteuthis opalescens*) since about 1990.

The overall abundance of larval fish by major groups displays a different pattern, abundance being generally high from the 1960s through the 1980s ($\bar{x} = 666 \text{ } 10\text{m}^{-2}$) and about 50% lower at the beginning of the time series in the 1950s ($\bar{x} = 320 \text{ } 10\text{m}^{-2}$) and in the 1990s ($370 \text{ } 10\text{m}^{-2}$). Larval abundance has continued to decline more recently, such that abundance since 2000 ($\bar{x} = 200 \text{ } 10\text{m}^{-2}$) is now only 30% that from 1960-89 (Fig. 3). The decline in recent decades is largely due to the decline of northern anchovy and Pacific hake, the most abundant taxa in the data set, but there was still a 31% decline between the decades of 1972-81 and 2002-11 in overall larval fish abundance with these two species removed. Non-commercial fishes comprise a significant proportion of larval fish abundance, with the mesopelagic fishes alone comprising 29.1% of total numbers.

For the commercially important fishes that spawn in the CalCOFI survey area, there was generally not a significant relationship between their fishery landings and larval fish abundance (Fig. 4). It appears that the Pacific hake fishery has been carried out since the 1990s largely during a period of low stock size, and the peak of the jack mackerel fishery in the 1980s also appears to coincide with a period of reduced spawning stock size. The collapse of the Pacific sardine fishery in the 1950s can also be seen to follow from a period of continued fishing during a period of sharply reduced spawning stock. The northern anchovy fishery, on the other hand, declined in advance of the decline in stock size, apparently due to loss of market (CDFW 2015).

However, there were significant relationships between larval abundance in the CalCOFI time series and spawning stock biomass estimates from stock assessments for northern anchovy, Pacific sardine and Pacific mackerel (Fig. 5). These relationships, along with recent acoustic estimates for the biomass of jack mackerel (Zwolinski et al. 2012) and migratory and non-migratory mesopelagic fishes (Davison et al. 2013, 2015) enabled us to estimate time series for the spawning stock biomass of these major planktivore groups since 1951 (Fig. 6). Mean biomass from 1951 through 2011 for these taxa in the southern CCLME are: Pacific sardine, 0.38 million metric tonnes (Mt); northern anchovy, 0.32 Mt; Pacific mackerel, 0.25 Mt; jack mackerel, 0.91 Mt; diel migratory mesopelagic fishes, 6.61 Mt; and non-migratory mesopelagics, 2.59 Mt. Mesopelagic fishes dominate the biomass of planktivores in the CCLME, comprising about 83% of the total biomass, so their fluctuations dominate this time series (Fig. 6). The biomass of mesopelagic fishes (both migrators and non-migrators) exhibits considerable low-frequency variability in the southern CCLME, with periods of low biomass (B) from 1951 until the mid-1960s ($\bar{x}_B = 6.94 \text{ Mt}$), relatively high biomass from the late 1960s through the 1990s ($\bar{x}_B = 12.21 \text{ Mt}$), followed by a decline since about 2000 ($\bar{x}_B = 7.34 \text{ Mt}$). The mean biomass of mesopelagic fishes was thus reduced about 69% over those two periods of low abundance relative to their biomass in the intervening period. There were no significant trends or apparent patterns to the overall biomass of epipelagic planktivores, although individual taxa underwent periods of relatively high and low biomass.

Although fish biomass is highly dominated by mesopelagics, plankton consumption by epipelagic and mesopelagic fishes in the southern CCLME appears roughly comparable (Table 1, Fig. 7), because the metabolic rate of epipelagic fishes, such as sardine, is more than 3-fold higher than for mesopelagic migratory fishes and about an order of magnitude higher than for non-migratory fishes (Childress et al. 1980). The periods from the late 1950s to mid-1960s and since about 1999 have experienced dramatically reduced plankton consumption, primarily due to reduced abundance of mesopelagic diel migrators, while the 1990s experienced relatively high plankton consumption rates due to the high biomass of mesopelagic migrators and briefly of jack mackerel. The 1970s and 1980s were also periods of anomalously high plankton consumption due to the relatively high abundance of first, northern anchovy, followed by Pacific mackerel (Fig. 7). Overall the time series exhibits considerable decadal-scale variability related to the ebb and flow of the various planktivore populations. However, several of these “waves” are particularly pronounced because several groups contributed to them at the same time. Thus the period since the end of the 1990s has experienced reduced abundance of mesopelagic fishes, northern anchovy and both mackerels, whereas the mid- to late-1990s saw all these groups (except northern anchovy) at relatively high levels of abundance.

DISCUSSION

Mean annual larval fish abundance was consistently significantly correlated with estimates of stock biomass from stock assessments and acoustic surveys but uncorrelated with time series of fishery landings for the CCLME either in aggregate or on a species-by-species basis. Indeed the overall trend of fishery landings in the CCLME is virtually opposite to the trend observed in the larval abundance time series. Regional fishery landings have tended to increase since the 1950s and to have stabilized at relatively high levels since about 1995, whereas the biomass for several major fish groups has declined dramatically in recent decades. These declines appear related to changing ocean conditions (Koslow et al. 2013, submitted; Miller and McGowan 2013). The decline of a broad suite of midwater fishes in the southern CCLME appears to have been in response to declining midwater oxygen concentrations and an expanding oxygen minimum zone (Koslow et al. 2011). Furthermore, there has been a marked decline in taxa identified as having cool-water affinities (Moser et al. 1987)), which include several of the most abundant larval fishes in the time series: northern anchovy, Pacific hake, rockfishes, and two highly abundant midwater fishes that were not correlated with changing oxygen conditions, the northern lampfish and California smoothtongue (Koslow et al. 2013). The decline is consistent with the massive decline (>70%) reported for the region's nearshore cool-water assemblage sampled from power-plant cooling-water intakes since 1972 (Miller and McGowan 2013). Both time series are correlated with a warming trend in the region's sea-surface temperatures and declining CalCOFI zooplankton displacement volumes (Koslow et al. submitted).

Several factors may be responsible for this disparity between the region's fishery landings and fishery-independent time series. First, many taxa that declined are not commercially exploited or are underexploited. These include the mesopelagic fishes, none of which are exploited, and northern anchovy, which may have been underexploited historically in the CCLME. Secondly, relatively stable commercial fishery landings have been maintained by re-focusing effort on species that increased during this period, such as Pacific sardine, or species that were previously under-exploited, such as the market squid. It is also possible that fishery quotas and landings have not fully reflected declining stock status, such as for Pacific sardine in the 1950s and Pacific hake more recently. However, regardless of the cause, it is apparent that reliance on fishery landings data may lead to a highly misleading view of the state of marine ecosystems: the dramatic decline (on the order of 70%) of larval marine fishes in the CCLME is not apparent from the commercial landings data.

A major question for future investigation is whether the major trends observed in the CalCOFI ichthyoplankton time series, such as the declines of mesopelagic fishes and of taxa with cool-water affinities are largely restricted to the southern CCLME or reflect trends over a larger area. The CalCOFI survey region is an ecotone, where fish faunas (particularly mesopelagics) with cool-water and warm-water affinities meet (Moser and Watson 2006). It may therefore be particularly sensitive to climate forcing. On the other hand, the impacts of climate forcing, such as ENSO events or the PDO, are often documented for zooplankton and fishes over the entire CCLME (Chelton et al. 1982, Hare and Mantua 2000). Many of the mesopelagic fishes have extensive geographic ranges: taxa with cool-water affinities, such as the northern lampfish, may extend into Alaskan waters and across the Transition Zone to the Northwest Pacific (Moser 1996, Moser and Watson 2006). Whether the decline of such taxa in the southern CCLME indicates a retreat of this fauna from the southernmost extent of its range or reflects a broad

decline over the extent of their range has profound implications for the ecology and biogeochemistry of the North Pacific Ocean.

This issue is exemplified by a recent review of global fisheries that upheld the CCLME as a region whose stocks were notably re-building (Worm et al. 2009). This is clearly not apparent in the CalCOFI ichthyoplankton data, but their data were derived largely from trawl surveys, fisheries, and stock assessments for taxa in the northern CCLME. It would clearly be useful to examine more northerly ichthyoplankton time series to assess the coherence (or lack thereof) of trends between the northern and southern CCLME.

Our preliminary estimates of plankton consumption in the southern CCLME indicate that the small epipelagic plankton-feeders, in particular the Pacific sardine, that have historically dominated fisheries research in the southern CCLME are not in fact ecologically dominant as consumers of zooplankton. This is apparent from acoustic surveys of the region, which show that small pelagics only dominate in the near-coastal region, with mesopelagic fishes dominant across much of the CCLME, which extends several hundred kilometers off the coast (Koslow et al. 2011). Acoustic/trawl surveys, combined with the ichthyoplankton time series, indicate that the mean biomass of mesopelagic fishes in the CCLME since 1951 (9.2 Mt) has been almost 5-fold higher than that of the principal epipelagic planktivores (Pacific sardine, northern anchovy and the two mackerels), and that the plankton consumption of mesopelagic and epipelagic planktivores is of similar magnitude. This indicates that the CCLME is not a “wasp-waisted” ecosystem (*sensu* Cury et al. 2000), with Pacific sardine or northern anchovy dominating zooplankton consumption by fishes. Mesopelagic planktivores represent a diverse assemblage, whose role at this trophic level clearly must be included in ecosystem models of the CCLME (and no doubt other LMEs) that seek to simulate the impact of fish predation on the zooplankton. However, the trophic pathways from mesopelagics to higher trophic levels remain unresolved: whether the flow is predominantly to mesopelagic predators, such as stomiid fishes and mesopelagic squids (Sutton and Hopkins 1996) or to epipelagic predators, such as various marine mammals, seabirds, and piscivorous fishes. Mesopelagic fish production is massive on a global scale and whether it represents a trophic cul de sac, permanently shunted to the deep pelagic realm, or whether a significant proportion returns to epipelagic ecosystems has considerable implications for global ecosystem dynamics and biogeochemistry.

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401 FIGURE LEGENDS.

402 Figure 1. The region off California, Oregon and Washington from which fishery landings were
 403 obtained for the California Current Large Marine Ecosystem (CCLME). The standard CalCOFI
 404 survey stations are shown from San Francisco south, which are surveyed in winter and spring for
 405 Pacific sardine. The large box shown in dash-dot lines is the area included in estimation of both
 406 larval abundance and mesopelagic fish biomass. The dashed lines around most of the six
 407 southern-most CalCOFI transects enclose the core stations used to estimate larval abundance in
 408 Koslow et al. (2011, 2013).

409 Figure 2. Fishery landings from the CCLME by major group, 1950-2013. (Source: US
 410 commercial fishery landings for California, Oregon and Washington from NOAA (2015).

411 Figure 3. The mean annual abundance of fish larvae (ind. 10 m⁻²) from CalCOFI surveys, 1951-
 412 2011.

413 Figure 4. Time series of fishery landings (in blue) and larval fish abundance (in green) for
 414 northern anchovy, Pacific sardine, Pacific hake, and jack mackerel, 1951-2011. The
 415 nonparametric correlation (Spearman's ρ) between the two time series is shown and its
 416 significance level (ns: not significant). Only positive correlations were tested for significance.

417 Figure 5. Linear regression relationships between mean annual larval abundance in the CalCOFI
 418 time series and stock estimates of spawning stock biomass for Pacific sardine, northern anchovy
 419 and Pacific mackerel.

420 Figure 6. (Upper) Time series of the biomass of the major planktivores in the CCLME 1951 -
 421 2011: Pacific sardine, northern anchovy, Pacific mackerel, jack mackerel, diel migratory and
 422 non-migratory mesopelagic fishes. (Lower) Pie chart showing the proportion of mean biomass of
 423 these planktivores groups over the period.

424 Figure 7. (Upper) Time series (1951-2011) of anomalies from the mean of estimated plankton
 425 consumption by major epipelagic planktivores (Pacific sardine, northern anchovy, Pacific and
 426 jack mackerel) and diel migratory and non-migratory mesopelagic planktivores. (Lower) Pie
 427 chart showing the proportion of mean annual consumption by group over this period.

428

429 Table 1. Estimated mean plankton consumption (1951-2011) in millions of metric tonnes (Mt) by
430 major planktivores in the southern California Current.

431

Planktivore group	Prey consumption (Mt yr⁻¹)
Pacific sardine	4.9 (9%)
Northern anchovy	4.7 (9%)
Pacific mackerel	3.8 (7%)
Jack mackerel	12.1 (22%)
Vertical migrators	27.1 (49%)
Non-migrators	2.5 (5%)
TOTAL	55.1

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 437 obtained for the California Current Large Marine Ecosystem (CCLME). The standard CalCOFI
 438 survey stations are shown from San Francisco south, which are surveyed in winter and spring for
 439 Pacific sardine. The large box shown in dash-dot lines is the area included in estimation of both
 440 larval abundance and mesopelagic fish biomass. The dashed lines around most of the six
 441 southern-most CalCOFI transects enclose the core stations used to estimate larval abundance in
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Figure 2. Fishery landings from the CCLME by major group, 1950-2013. (Source: US commercial fishery landings for California, Oregon and Washington from NOAA (2015).

Figure 3. The mean annual abundance of fish larvae (ind. 10 m⁻²) from CalCOFI surveys, 1951-2011.

Figure 4. Time series of fishery landings in metric tonnes (t) (in blue) and larval fish abundance (ind. 10 m⁻²) (in green) for Pacific sardine, northern anchovy, Pacific hake, and jack mackerel, 1951-2011. The nonparametric correlation (Spearman's ρ) between the two time series is shown and its significance level (ns: not significant). Only positive correlations were tested for significance.

Figure 5. Linear regression relationships between mean annual larval abundance in the CalCOFI time series and stock estimates of spawning stock biomass for Pacific sardine, northern anchovy and Pacific mackerel.

Figure 6. (Upper) Time series of the biomass of the major planktivores in the CCLME in millions of metric tonnes (Mt) 1951 - 2011: Pacific sardine, northern anchovy, Pacific mackerel, jack mackerel, diel migratory and non-migratory mesopelagic fishes. (Lower) Pie chart showing the proportion represented by the mean biomass of these planktivores groups over the period. Both panels use the same color legend.

Figure 7. Time series (1951-2011) of anomalies from the mean of estimated plankton consumption by major epipelagic planktivores (Pacific sardine, northern anchovy, Pacific and jack mackerel) and diel migratory and non-migratory mesopelagic planktivores. The pie chart at bottom shows the proportion of mean annual consumption by group over this period: VM: (mesopelagic) vertical migrators; NM: (mesopelagic) non-migrators.