Strictly for the Birds?

On Ecosystem Services of Forage Fish

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Abstract

Small pelagic fish like sardine, anchovy and herring feed on zooplankton and are in turn prey for fish higher up in the food chain. They are therefore expected to play a vital role in transfer of energy between levels in the food chain. Some stocks of small pelagics are extremely large and subject to very substantial fluctuations caused by environmental factors. They are also very vulnerable to exploitation due to schooling behavior and highly efficient fishing technology. Several such stocks crashed in the 20th century as a result of heavy exploitation and/or adverse environmental changes. The effect of four such stock crashes on other fisheries are reviewed and found to be limited or nonexistent. This puts into perspective a recent report from the Lenfest Foundation, which examines small pelagics and their role in the ecosystem and finds that certain sea bird populations have been severely affected by exploitation of small pelagics. The report recommends more conservative management of small pelagics to limit the effects on predators, but makes no effort to weigh this against the contribution of forage fish to food production.

Keywords: Small pelagics, fish stock collapses, forage fish, ecosystem based fisheries management.

1. INTRODUCTION

In April 2012, the Lenfest Foundation published a report entitled "Little Fish, Big Impact" ([1] hereafter the Lenfest Report). The report discusses the role of forage fish in the ecosystems of the oceans. Forage fish is an expression used for small, pelagic fish that are eaten by other fish higher up in the food chain. These small fish live on plankton and play an important role in transferring biomass and energy between levels in the food chain. The title of the report appeared well chosen; the fish are small, but due to their role in the transfer of energy their impact could be big.

There are further reasons why one should be concerned about forage fish. One is that there are relatively few species involved, while individual stocks can be very large. Furthermore, historical records have shown that these species are prone to large fluctuations caused by environmental variability beyond human control [2]. Hence, when the stocks of these fish are at low levels, the amount of biomass transferred further up in the food chain could be severely limited. This has given rise to the "wasp-waist" metaphor as a description of an ecosystem critically dependent on a few strategic species in the middle of the food chain [3,4], but the relevance of this metaphor is not uncontested [5]. A recent review of the role of forage fish puts it this way ([4] p. 12):

> "… this massive population of *wasp waist* forage fish performs a crucial role in the overall function of its entire ecosystem. … Typically these populations of small pelagic planktivores experience wide inter-annual variability in reproductive success. Because of their short life spans, this results in extreme variability in their population sizes that has major effects on the trophic levels above, which depend on the wasp waist populations as their major food source, and also on the trophic levels below which are fed upon by the wasp waist populations. Thus the major control on the productivity of the entire complex of species in these ecosystems may be neither ''bottom up'' nor ''top down'' but rather ''both up and down from the middle."

Yet another reason why we need to manage the forage fish species carefully is that the behavior of these fish together with modern fishing technology makes them very vulnerable to fishing. They typically aggregate and migrate in large, dense shoals, which is believed to be an evolutionary response minimizing the effects of predation. This is due to the "predator saturation" effect; one or a few predators are able to consume only a small part of a large shoal of fish, leaving plenty to escape. In contrast, modern fishing fleets are extremely efficient predators; they are equipped to find the shoals of fish wherever they are and to encircle them with enormous nets and pump them out of the water, leaving little or nothing behind. It has long been known that catch per unit of effort is next to useless as a monitor of the stock size under these circumstances [6], and so both industry and managers may have little clue about what is happening to the stocks until it is too late.

The twentieth century was a period of rapid technological progress in fisheries and also of some spectacular crashes of stocks of forage fish, brought on by a confluence of rapid technological progress and adverse environmental circumstances. Nevertheless, these crashes had little or no effect on the catches of their known or potential predators. This is curious, given the acknowledged role of the forage fish in the transfer of energy.

In this paper we shall review the impact on other fisheries of four well-known crashes of forage fish stocks; the Pacific sardine, the Norwegian spring-spawning herring, the South African pilchard, and the Peruvian anchovy. We shall do this by correlating catches of known and hypothetical predators of these stocks with the stocks that crashed (for the pilchard and the anchovy, we shall use catches from these stocks as proxies). As will be seen, such correlation is largely absent.

Given the very limited impact from these stock collapses on catches of other fish, it is rather surprising that the Lenfest Report recommends a considerably more conservative exploitation of forage fish than practised presently. It turns out that this recommendation is largely driven by adverse impacts on sea bird populations and other iconic animals and is made without any explicit tradeoff between these and captures of forage fish for food production. We shall return to this in the concluding section, after discussing the said four stock crashes.

2. FOUR STOCK COLLAPSES

2.1 The Pacific Sardine

In the 1930s and early 1940s annual landings of Pacific sardine in California exceeded 400,000 tonnes. Then they fell to almost nothing in less than ten years (1946-52). Needless to say, this caused a major disruption to the canning and fish meal industries that were based on the sardine [7]. After 1960 the sardine fishery virtually disappeared, and in 1973 it was closed, but reopened when the stock recovered in the 1990s.

In its heyday, the Pacific sardine fishery was by far the biggest fishery in California. When the sardine stock is in good condition, it probably is the largest single fish stock in the Northeast Pacific Ocean. It is thought to play a crucial role in the California current ecosystem as forage for a multitude of species higher up in the food chain [8]. Given this critical role, one would expect the sardine collapse to have caused a severe decline of fish stocks higher up in the food chain. Yet, if one looks at the landings statistics, it is difficult to detect anything like that. Figure 1 shows the sardine stock and the total landings of 23 species which have been identified as predators of anchovy and sardine.[1] The landings of these predator species increased after the sardine collapse and fell as the sardine stock recovered in the 1990s, contrary to what one would expect.

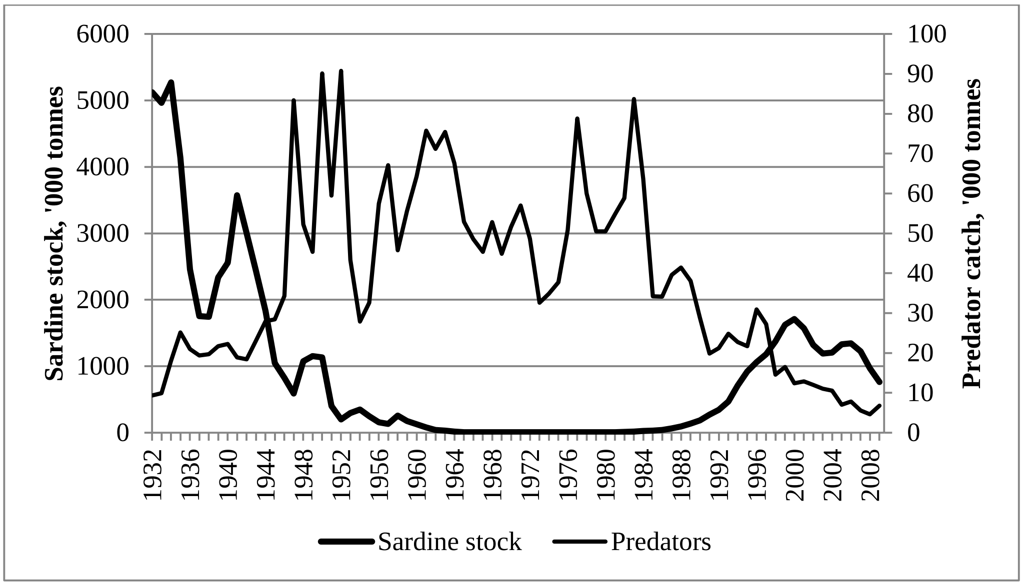

Figure 1

A reason why we see no trace of falling landings of sardine predators after the collapse of the sardine could be increased abundance of other forage fish that could also serve as a source of food for sardine predators. Figure 2 shows the stocks of Pacific sardine, Northern anchovy and Pacific mackerel. We see that the stocks of the latter two increased as the sardine disappeared, and fell when it reappeared. This indicates that the two other forage fish stocks expanded into an ecological void left by the disappearing sardine. Nevertheless, they did not come close to attaining the previous level of the sardine stock, but did rise to a level comparable to where the sardine has been in recent years.

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[1] Albacore tuna (*), barracuda (*), bluefin tuna (*), bonito (*), butterfish, California halibut (*), cabezon, giant sea bass (*), jack mackerel (*), ling cod (*), lobster, market crab, ocean whitefish (*), Pacific halibut (*), sablefish, salmon, scorpionfish (*), sheephead, skipjack tuna, swordfish (*), white croaker, white seabass (*), yellowfin tuna, and yellowtail (*). Those marked with (*) are identified as predators of anchovy in the Coastal Pelagic Species Fishery Management Plan ([9] Table 1.1.2-1), which states that these are also likely predators of sardine.

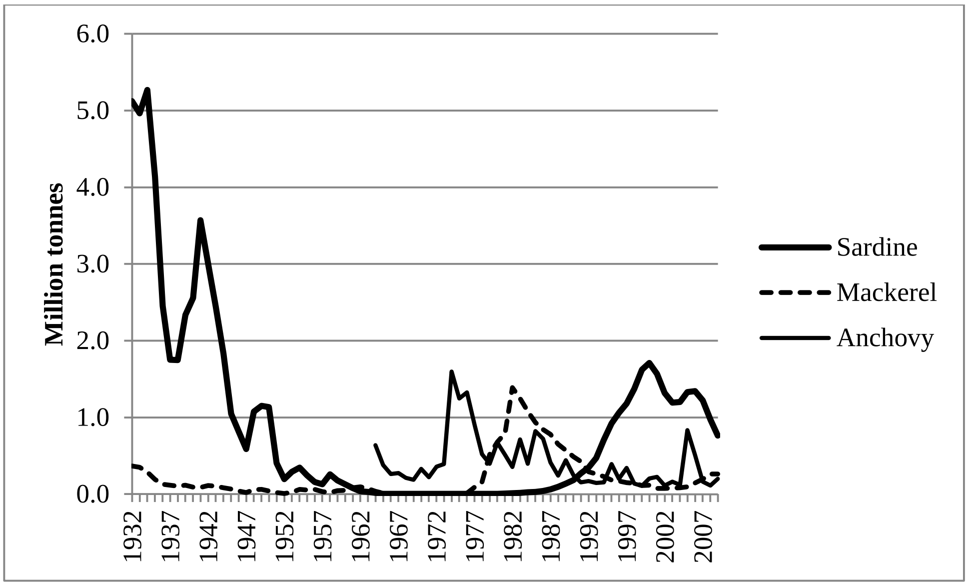

Figure 2

One reason why we see rising catches of sardine predators after the collapse of the sardine stock could be that the fishery for these species developed after the collapse, for reasons of marketing or technology. Clearly the sardine stock could not have been critical for these species, but it might still have been important. It is worthwhile, therefore, to look at sardine predators individually and investigate whether we find any relationship between catches of a predator species and the sardine stock. Ideally we would like to have time series of individual stocks to correlate with the sardine, but such data are simply not available; all we have are landings data. To some extent, landings data must reflect the abundance of the underlying fish stock. Landings cannot stay high indefinitely without the stock from which they are taken being reasonably healthy. If landings exceed the surplus growth of the stock year after year the stock will sooner or later collapse. A nearly or fully extinct stock sustains no fish landings.

If a predator stock depends crucially on the sardine stock, there would be a positive correlation between the sardine stock and landings of the predator. Table 1 shows the results of linear regressions of predator landings on the sardine stock. There are more significantly negative regression coefficients than positive, which is not meaningful for a predator species, but would be expected for species competing with the sardine (we get this for anchovy and sardine; cf. Figure 2). There are five species for which we get a significantly positive regression coefficient (barracuda, Bluefin tuna, giant sea bass, ocean whitefish, and Pacific halibut). All of these are identified as predators of anchovy and sardine.

Table 1

Sign of coefficient in a regression of predator landings on sardine biomass. * (**,***) denotes significance at the 5 (1, 0.1) percent level.

Positive	**Insignificant**	**Negative**
Barracuda***	California halibut	Albacore***
Bluefin***	Cabezon	Bonito***
Giant sea bass***	Hake	Butterfish***
Ocean whitefish***	Lobster	Jack mackerel***
Pacific halibut***		Ling cod***
		Market crab***
		Sablefish***
		Salmon**

Figure 3 shows the biomass of the sardine stock and the landings of the five sardine predators found to be positively correlated with the sardine stock, for the period 1932-2009. The landings of four of these collapsed with the sardine stock (barracuda, giant sea bass, ocean whitefish, and Pacific halibut). The landings of Bluefin tuna have been highly erratic, and the correlation with the sardine stock appears spurious; the Bluefin is a highly migratory species and probably not critically dependent on the sardine as a source for food. Barracuda and ocean whitefish recovered to some extent with the sardine stock in the 1990s, while landings of giant sea bass and Pacific halibut have remained low.

The decline in landings of the four species was several orders of magnitude less than the decline of the sardine stock. The latter collapsed from five million tonnes to next to nothing, landings of barracuda by about one thousand tonnes, Pacific halibut 400 tonnes, giant sea bass 100 tonnes, and ocean whitefish 70 tonnes, altogether less than two thousand tonnes, less than one pro mille of the decline of the sardine stock. Taking into account that landings from the plurality of stocks in California were unaffected by the sardine collapse and show a time pattern distinctly different from the five shown in Figure 3, it is difficult to conclude with anything other than the effect of the sardine collapse on the commercial fisheries of California was very limited indeed.

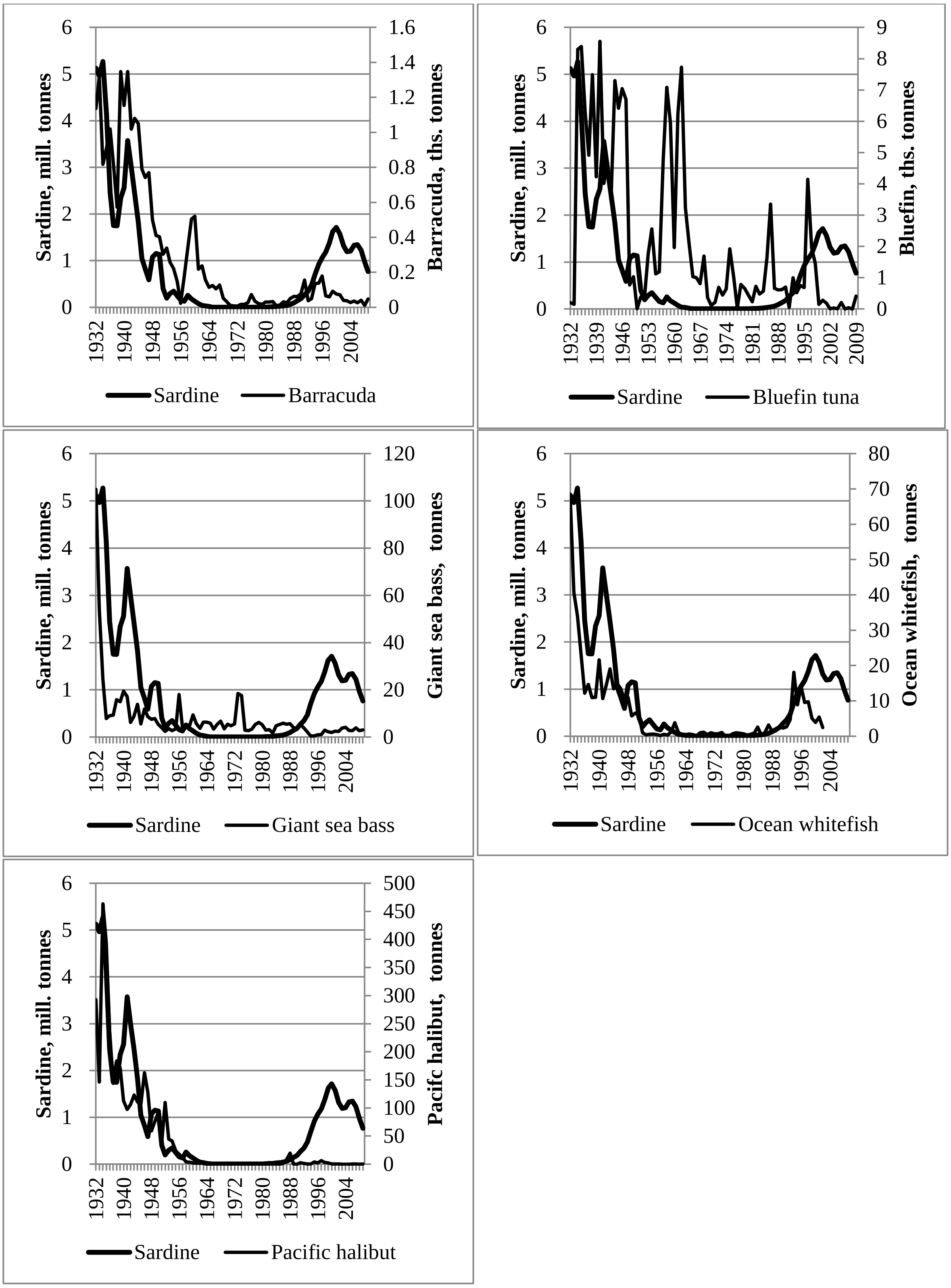
Sardine, mill. tonnes
Barracuda, ths. tonnes
0
1
2
3
4
5
6
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1932
1940
1948
1956
1964
1972
1980
1988
1996
2004
Sardine
Barracuda
Sardine, mill. tonnes
Bluefin, ths. tonnes
0
1
2
3
4
5
6
0
1
2
3
4
5
6
7
8
9
1932
1939
1946
1953
1960
1967
1974
1981
1988
1995
2002
2009
Sardine
Bluefin tuna
Sardine, mill. tonnes
Giant sea bass, tonnes
0
20
40
60
80
100
120
1932
1940
1948
1956
1964
1972
1980
1988
1996
2004
Sardine
Giant sea bass
Sardine, mill. tonnes
Ocean whitefish, tonnes
0
10
20
30
40
50
60
70
80
Sardine
Ocean whitefish
Sardine, mill. tonnes
Pacifc halibut, tonnes
0
50
100
150
200
250
300
350
400
450
500
Sardine
Pacific halibut

Figure 3

2.2 The Norwegian spring-spawning herring

The Norwegian spring-spawning herring stock collapsed in the late 1960s (Figure 4). In the early 1950s it was about 20 million tonnes, but declined gradually to almost nothing in the late 1960s. From the mid-1980s the stock recovered gradually and has in recent years varied between 10 and 15 million tonnes. Juvenile herring grow up in the Barents Sea and are known to be preyed on by cod. Mature herring spawn off the Norwegian coast and migrate towards Iceland during the summer in search for plankton.

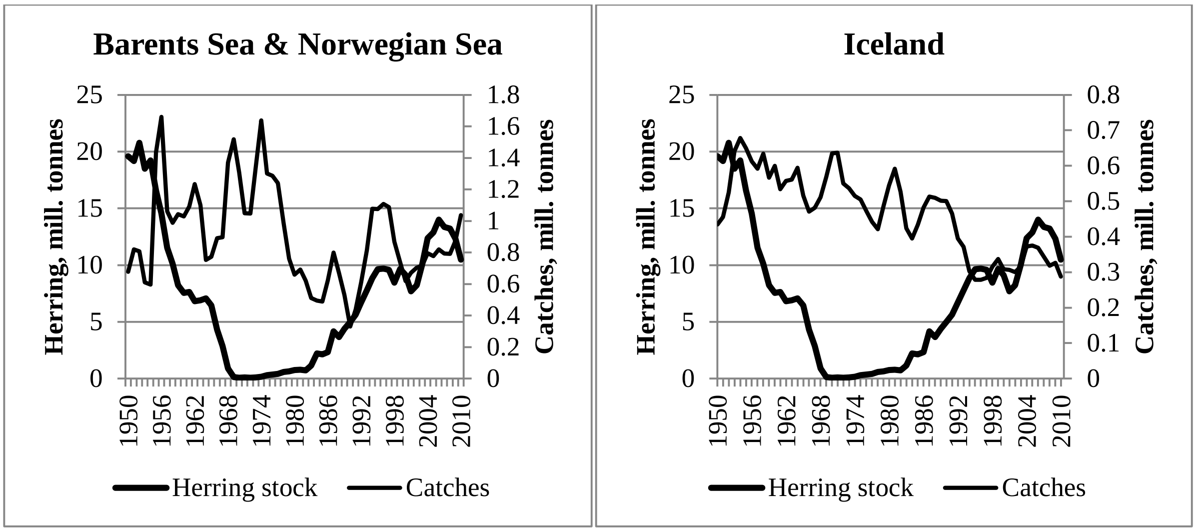

Figure 4

The herring collapse had severe effects on the catches of herring, which declined from being top landings from a single stock in Norway and Iceland to virtually nothing. The effect on catches of other fish was not noticeable. The three gadoids, cod, haddock and saithe, are the most important actual or potential herring predators captured in the Barents Sea, the Norwegian Sea, and at Iceland. There is no correlation between the herring stock and the captures of cod and haddock in the said areas, but a significantly negative correlation between the captures of saithe in these areas and the herring stock. Figure 4 shows the herring stock and the catches of all three species in the Barents Sea, the Norwegian Sea, and at Iceland. The absence of any correlation is evident. The catches of the three gadoids in the Barents Sea and the Norwegian Sea increased over the first years after the collapse of the herring stock. At Iceland the captures of these species have been in decline since the mid-1950s, irrespective of what has happened to the herring stock.

The absence of correlation between the herring stock and catches of cod in the Barents Sea and the Norwegian Sea is surprising, as cod are known to feed on young herring in the Barents Sea. The explanation probably lies in the blooming of the capelin stock, which apparently moved into the void vacated by the herring. Cod are also known to feed on capelin, so their total food supply may have been little affected by the collapse of the herring.

2.3 The South African pilchard

The South African pilchard (sardine) fishery collapsed in the late 1970s. Figure 5 shows the catches of pilchard and anchovy in South Africa and Namibia, taken from the FAO Fishstat database. Prior to 1987 there are only sporadic statistics for Namibia. At that time, what is now Namibia was administered by South Africa, so presumably fish catches from what is now Namibian waters were included in statistics for South Africa. We also see from Figure 5 that catches of anchovy increased in the wake of the collapse of the pilchard fishery, and so the pilchard seems to have been replaced by anchovy, much like what happened in California, but the catches of anchovy never reached the level of the peak catches of pilchard.

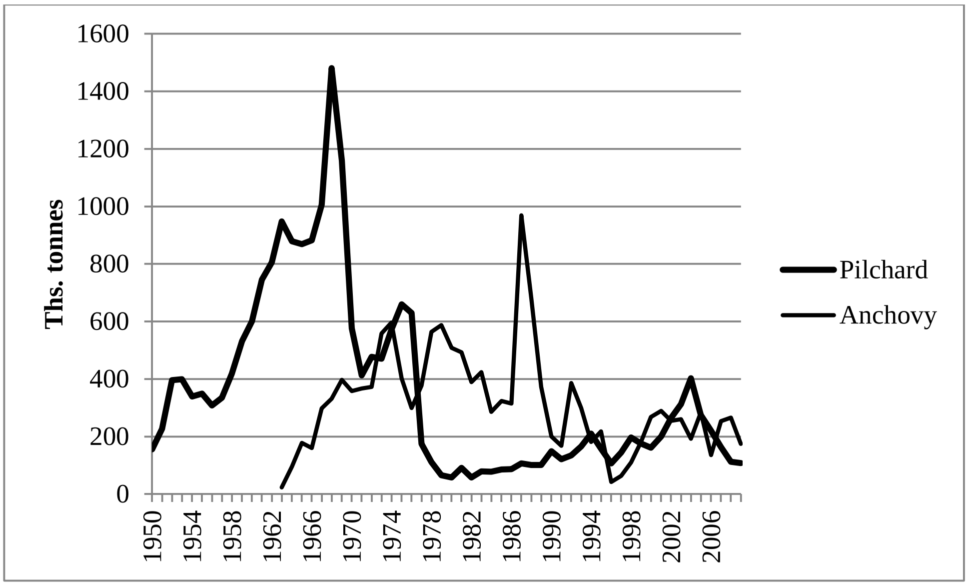

Figure 5

We do not have statistics for the pilchard stock, but the catches of pilchard probably are a reasonable proxy for the stock, as the case is for the Pacific sardine and the Norwegian spring-spawning herring. The FAO database shows substantial catches of several species, besides pilchard and anchovy, for South Africa from 1950 or soon after. Table 2 shows the sign of regression coefficients for these species and the catches of pilchard. Three of these are positive, involving rock lobster, chub mackerel, and what is labeled as “marine fish not elsewhere included”, here referred to as “unspecified fish.” Rock lobster is an unlikely predator of pilchard, as it lives on the bottom. Figure 6 shows the catches of pilchard versus the three species categories found to be positively correlated. For rock lobster we probably see a spurious correlation; the catches of rock lobster have been on a declining trend since the early 1950s, and the pilchard catches show a declining trend since the late 1960s. The catches of unspecified fish and of chub mackerel follow a pattern similar to the catches of pilchard, so for these the collapse of the pilchard seems to have led to a decline. The quantities involved are an order of magnitude less than the catches of pilchard, which is not unexpected, as 80-90 percent of biomass could be lost in the transfer between different levels of the food chain.

Table 2

Sign of coefficient in a regression of landings of different fish species on landings of pilchard. * (**,***) denotes significance at the 5 (1, 0.1) percent level.

Positive	**Insignificant**	**Negative**
Rock lobster***	Panga seabream	Hake***
Chub mackerel***		Horse mackerel***
Unspecified marine fish***		Kingklip**
		Snoek*
		Herring$^{*a)}$

a) 1964-2009.

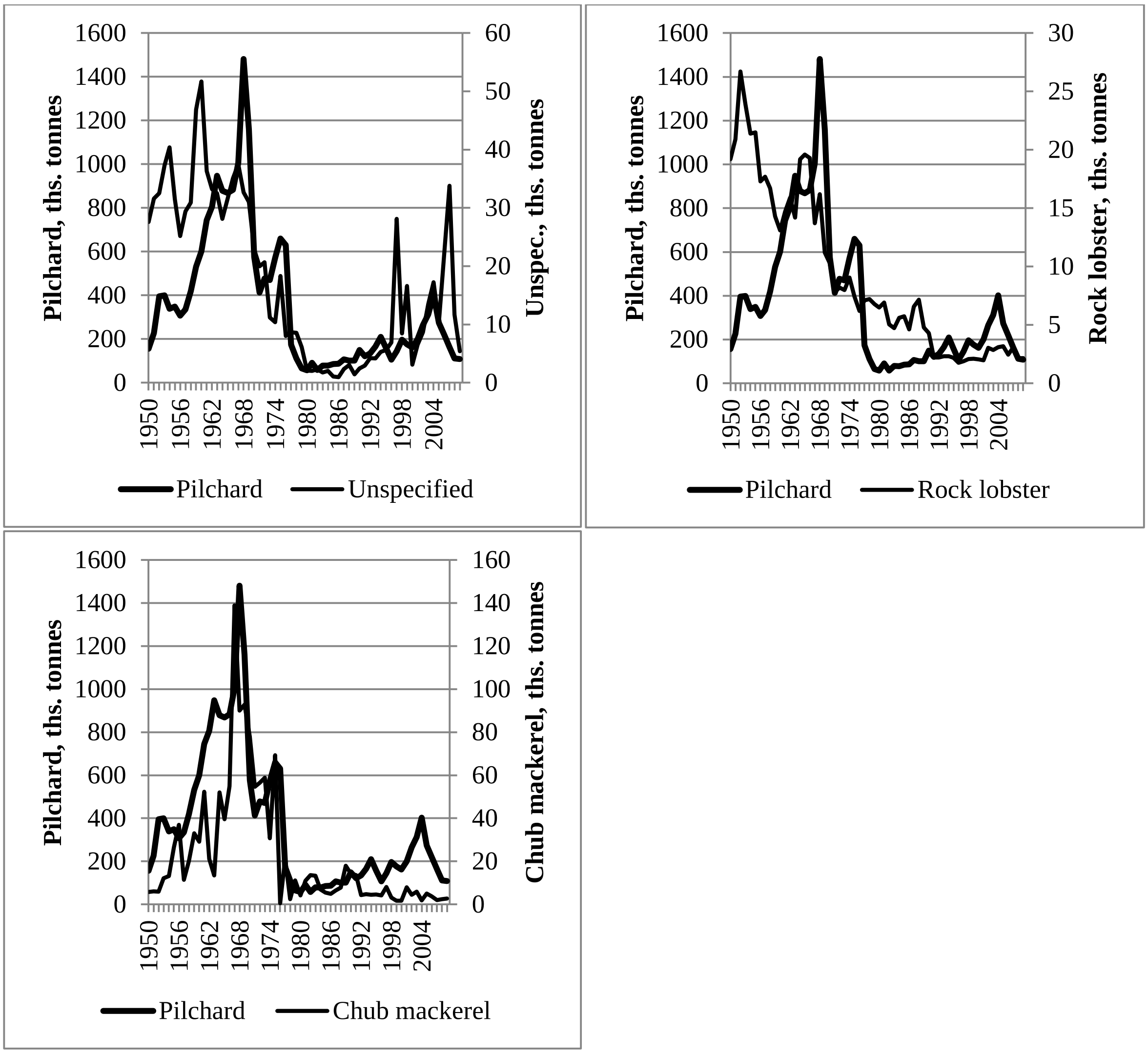

Figure 6

2.4 The Peruvian anchovy

The Peruvian anchovy fishery developed very rapidly in the late 1950s, as a result of the collapse of the sardine fishery in California [7], and crashed in the early 1970s due to a strong El Niño and lax management (Figure 7). It did not fully recover in the following years, and crashed again in 1983, under the influence of another El Niño. It did recover in the 1990s, and the impact of the strong El Niño in 1997 is in stark contrast to the previous two; the fish catches declined sharply in 1998, but recovered quickly. It appears that lessons had been learnt and a timely management imposed. Since the recovery in 1999 the annual catch has been 6-10 million tonnes. Catches of sardine replaced the lost catches of anchovy while the latter was down, albeit not entirely. Most probably the sardine stock moved into the void left behind by the anchovy.

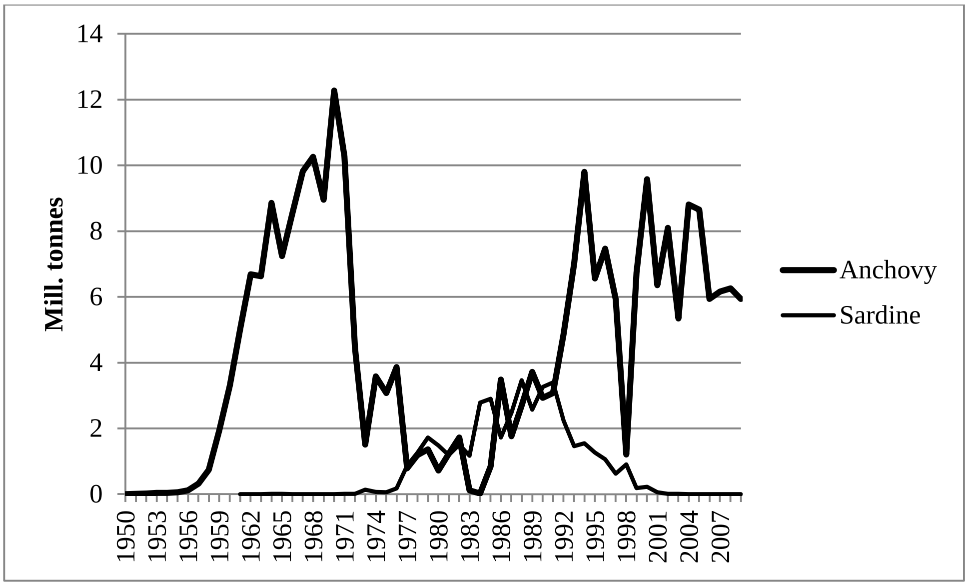

Figure 7

Table 3

Sign of coefficient in a regression of landings of different fish species in Peru on landings of anchovy 1960-2009. * (**,***) denotes significance at the 5 (1, 0.1) percent level.

Positive	**Insignificant**	**Negative**
Bonito**	Jack mackerel	Corvina drum*
Yellowfin*	Chub mackerel	Flatfishes**
	Groupers	Molluscs*
	Crabs	Mullets*
	Marine fish (unspecified)	Croaker**
	Menhaden	Smooth hounds*
	Sierra	Warehou**
	Rock seabass	
	Weakfish	
	Pompanos	
	Rays etc.	
	Sharks etc.[b)]	
	Skipjack tuna	
	Hake	
	Swordfish	

b) 1965-2009.

Table 3 shows the sign of regression coefficients for catches of various fish species in Peru versus catches of anchovy. The regressions were run for the period 1960-2009, as the anchovy fishery was not fully developed prior to 1960 (Figure 7). We get a significantly positive regression coefficient for only two species, bonito and yellowfin tuna. Both of these are indeed likely predators of anchovy.

Figure 8 shows the catches of these two species together with the catches of anchovy. The time profile of catches both of bonito and yellowfin tuna is quite similar to the time profile of the anchovy catches. It is therefore likely that the collapse of the anchovy affected the stocks of bonito and yellowfin tuna negatively, but the quantitative difference is enormous; the catches of anchovy fell by more than ten million tonnes from around 1970 to the early 1980s, while the catches of bonito declined by about 70,000 tonnes and the catches of yellowfin tuna less than 10,000 tonnes over the same period.

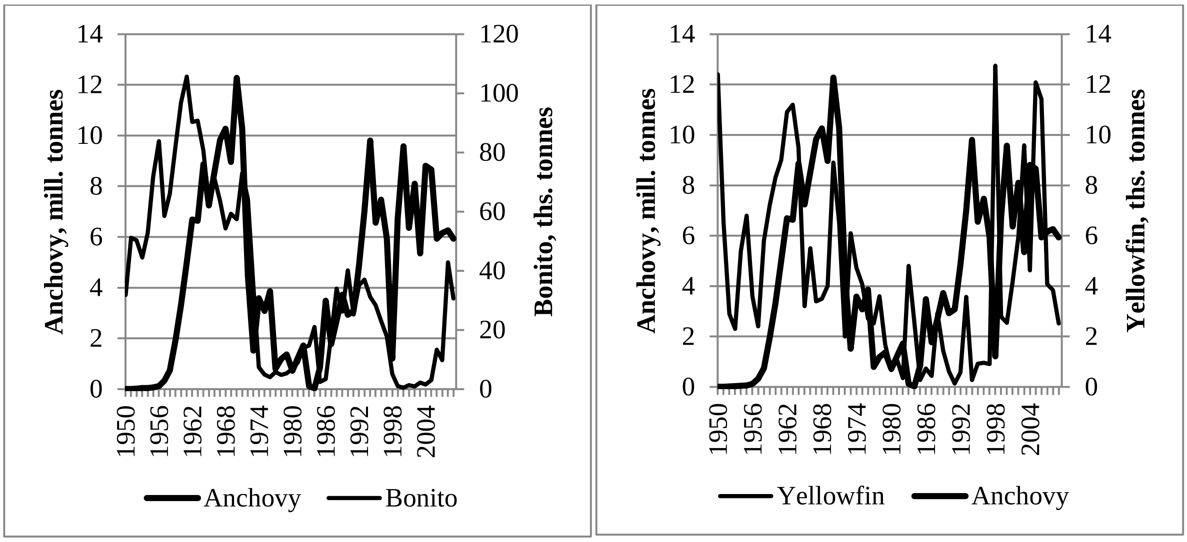

Figure 8

3. CONCLUSION

We have seen that the effect of four spectacular crashes of forage fish stocks on other commercial fisheries was limited to nonexistent. Hence, these stocks appear to play a much smaller role for fish higher up in the food chain than one might think. The latter apparently have a more varied food supply than depending on just one critical species. Furthermore, as one stock of forage fish crashes, others move in and bloom. This happened for all the four stocks we have considered, although apparently just partly and not fully; anchovy and mackerel replaced the sardine off California, capelin replaced herring in the Barents Sea, anchovy replaced pilchard off South Africa, and sardine replaced anchovy off Peru. This is likely to have replenished the food supply for species higher up in the food chain.

It would be curious if the collapse of the said stocks had no effect whatsoever further up in the food chain. Most likely it mainly affected marine mammals and sea birds. The latter appear to be particularly vulnerable to changes in the abundance of forage fish (Lenfest Report, p. 18). The Lenfest Report (p. 8) mentions specifically that the carrying capacity for African penguins has been reduced by 80-90 percent due to captures of forage fish in South Africa (and also due to competition from fur seals) [12], and (p. 48) that cormorants in Peru declined by almost 90 percent, due to the anchovy fishery [13] (further on sea birds, see [14-17]). As a matter of fact, the guano industry in Peru opposed the development of the anchovy fishery in the 1950s; the industry was well aware of where the supply of its raw material came from.

The Lenfest report recommends the adoption "of harvest strategies and management measures so that there is a greater than 95 percent chance that fishing on forage fish will not deplete any dependent predator population to levels that would meet the IUCN 'vulnerability criteria'" (p. 88). These are explained in a footnote; a population is "vulnerable to extinction … if it declined by 50 percent or more in the previous 10 years or three generations, whichever is longer, and where the causes of the reduction are clearly reversible and understood." It would seem that the Peruvian anchovy fishery and the South African fisheries for anchovy and sardines have long since passed that point. As mentioned above, both African penguins and the Peruvian cormorants seem to have declined a lot more than that, and so may other sea bird populations.

But should preservation of cormorants and other sea birds trump everything else when it comes to evaluating the utility of forage fish catches? After all, the fish meal and oil produced from the various forage fish we capture plays a vital role in raising the farmed fish, pigs and poultry that contribute to our food supply. At the very least we must acknowledge the tradeoff between preserving nature in a near-pristine state and using it to provide our food. Our planet is not just one gigantic theme park; it is also a place where we fetch our food and raw materials of various kinds. It would not be possible to feed a world population of seven billion and still growing without turning some areas into vast monocultures controlled with fertilizers and pesticides. That we need also to interfere with nature in the sea is neither surprising nor any different from what we do on land and something which we are unlikely to be able to do without.

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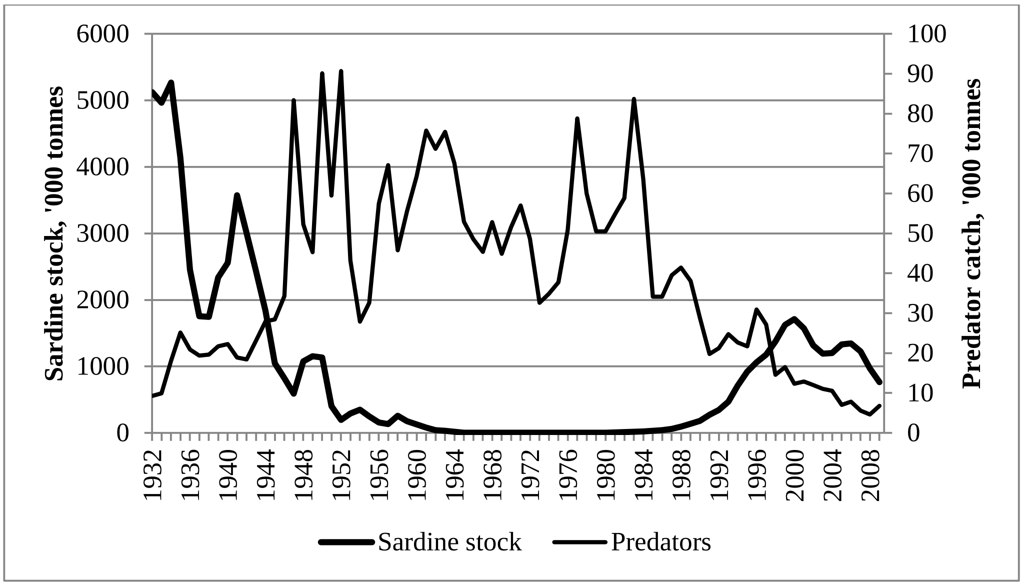
Sardine stock, '000 tonnes
0
1000
2000
3000
4000
5000
6000
Predator catch, '000 tonnes
0
10
20
30
40
50
60
70
80
90
100
1932
1936
1940
1944
1948
1952
1956
1960
1964
1968
1972
1976
1980
1984
1988
1992
1996
2000
2004
2008
Sardine stock
Predators

Figure 1

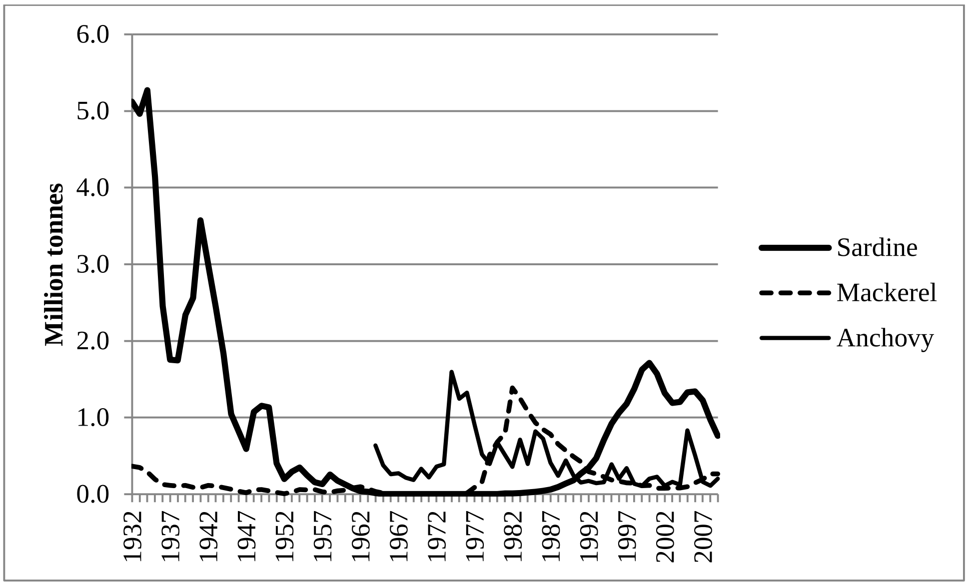
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Million tonnes
1932
1937
1942
1947
1952
1957
1962
1967
1972
1977
1982
1987
1992
1997
2002
2007
Sardine
Mackerel
Anchovy

Figure 2

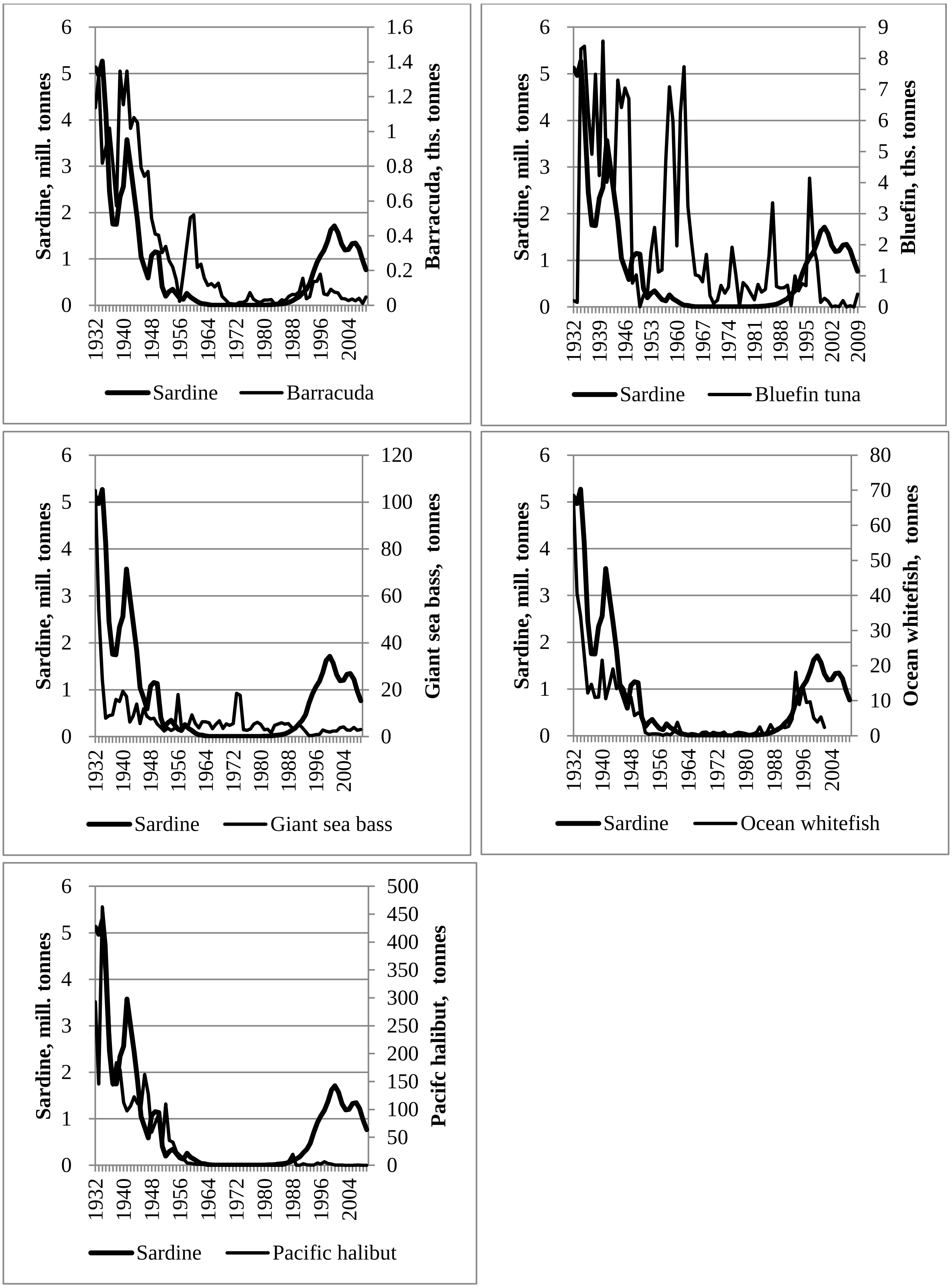
Sardine, mill. tonnes
Barracuda, ths. tonnes
Sardine
Barracuda
Bluefin, ths. tonnes
Bluefin tuna
Giant sea bass, tonnes
Giant sea bass
Ocean whitefish, tonnes
Ocean whitefish
Pacifc halibut, tonnes
Pacific halibut
1932
1940
1948
1956
1964
1972
1980
1988
1996
2004
1939
1946
1953
1960
1967
1974
1981
1995
2002
2009

Figure 3

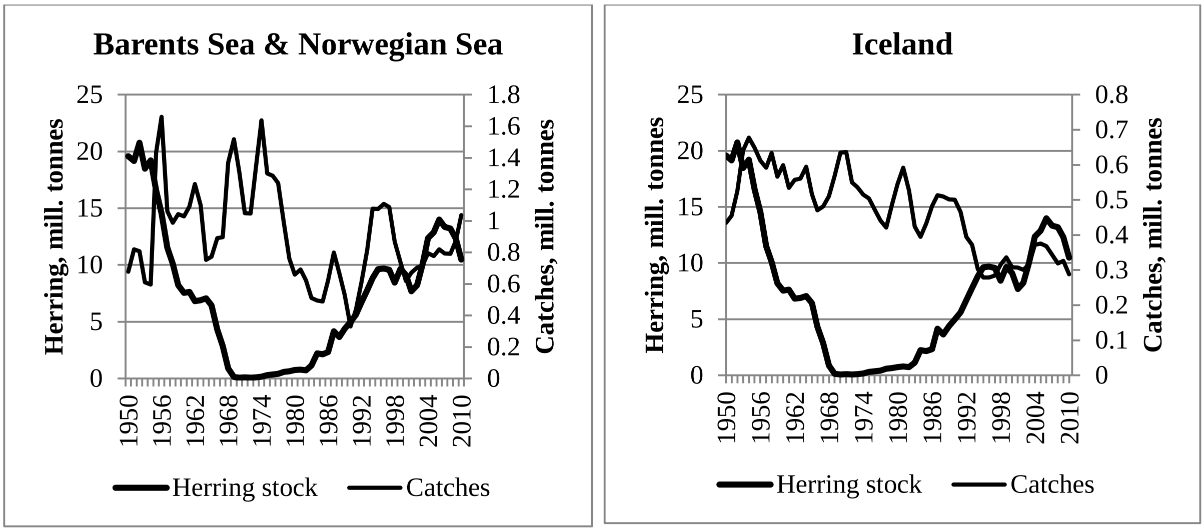
Barents Sea & Norwegian Sea
Herring, mill. tonnes
Catches, mill. tonnes
25
20
15
10
5
0
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
1950
1956
1962
1968
1974
1980
1986
1992
1998
2004
2010
Herring stock
Catches
Iceland
Herring, mill. tonnes
Catches, mill. tonnes
25
20
15
10
5
0
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1950
1956
1962
1968
1974
1980
1986
1992
1998
2004
2010
Herring stock
Catches

Figure 4

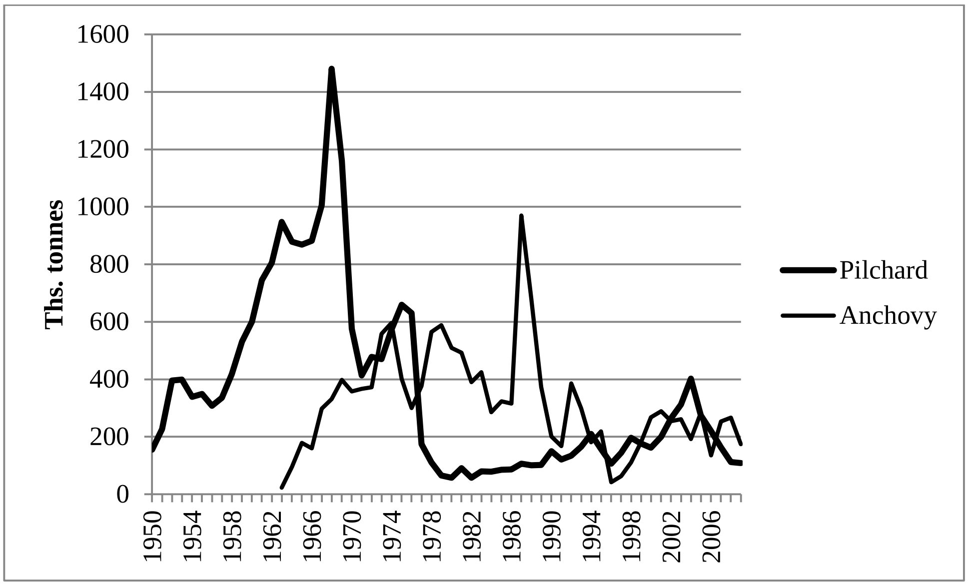
1600
1400
1200
1000
800
600
400
200
0
Ths. tonnes
1950
1954
1958
1962
1966
1970
1974
1978
1982
1986
1990
1994
1998
2002
2006
Pilchard
Anchovy

Figure 5

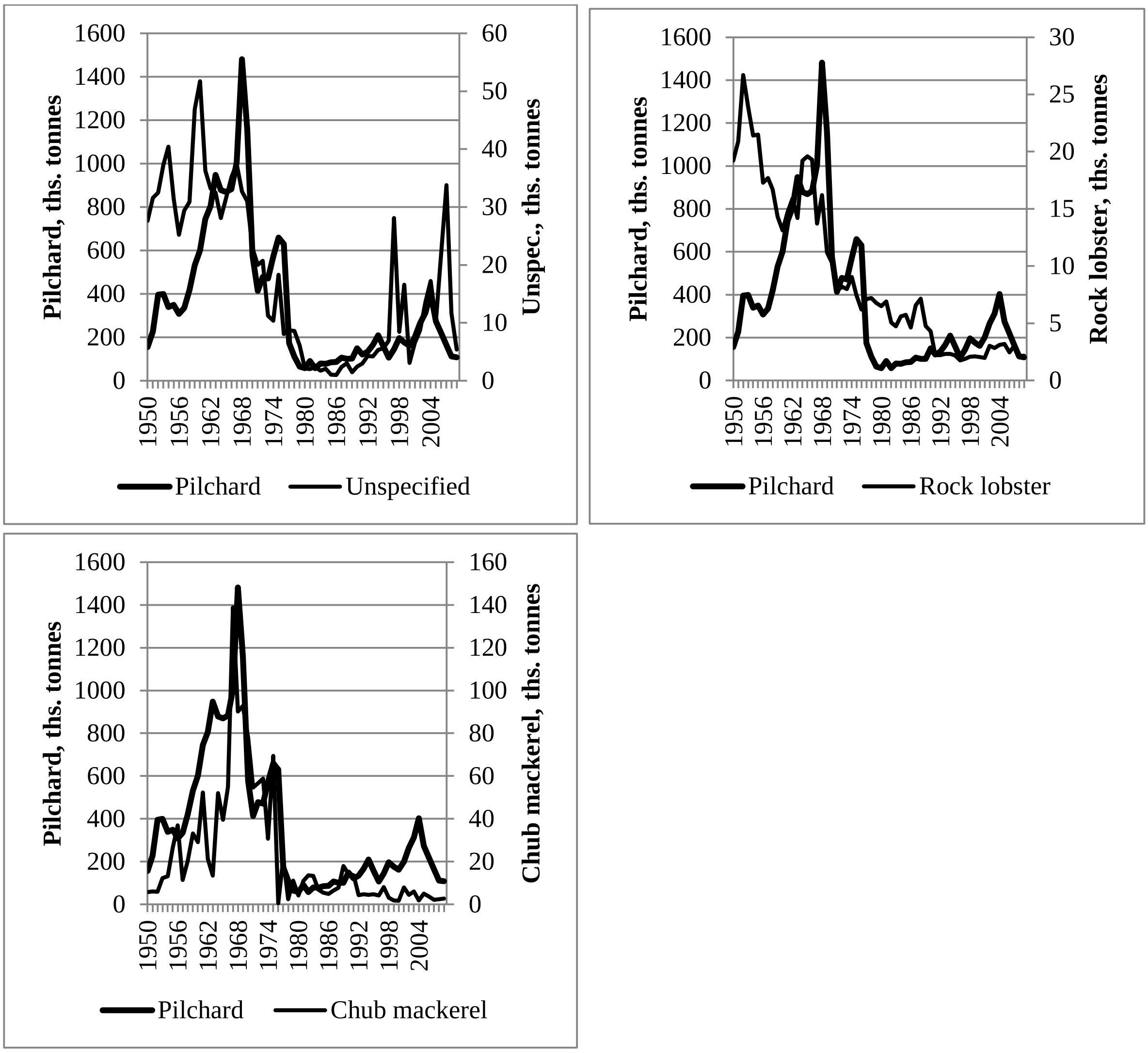
1600
1400
1200
1000
800
600
400
200
0
Pilchard, ths. tonnes
60
50
40
30
20
10
0
Unspec., ths. tonnes
1950
1956
1962
1968
1974
1980
1986
1992
1998
2004
Pilchard
Unspecified
30
25
20
15
10
5
0
Rock lobster, ths. tonnes
Pilchard
Rock lobster
160
140
120
100
80
60
40
20
0
Chub mackerel, ths. tonnes
Pilchard
Chub mackerel

Figure 6

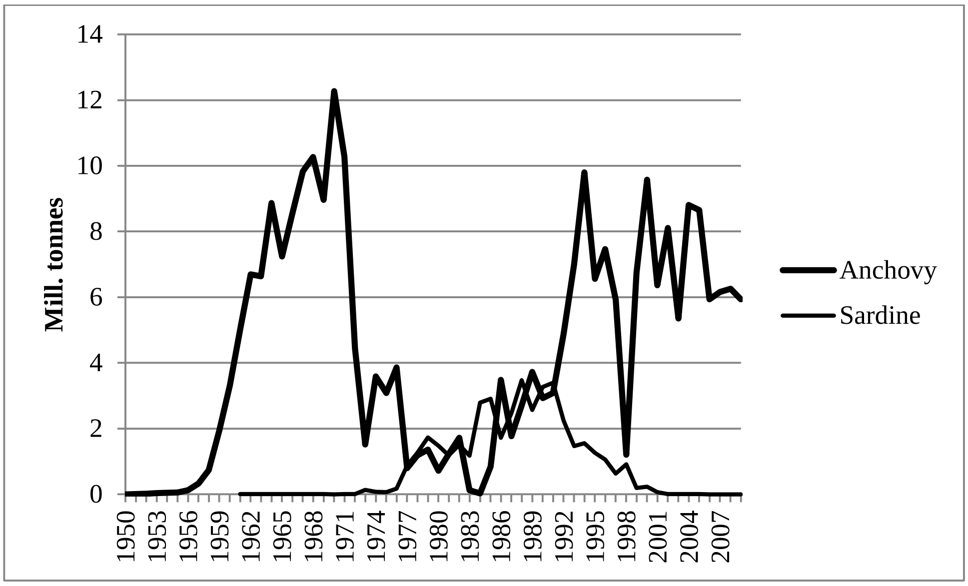
14
12
10
8
6
4
2
0
Mill. tonnes
1950
1953
1956
1959
1962
1965
1968
1971
1974
1977
1980
1983
1986
1989
1992
1995
1998
2001
2004
2007
Anchovy
Sardine

Figure 7

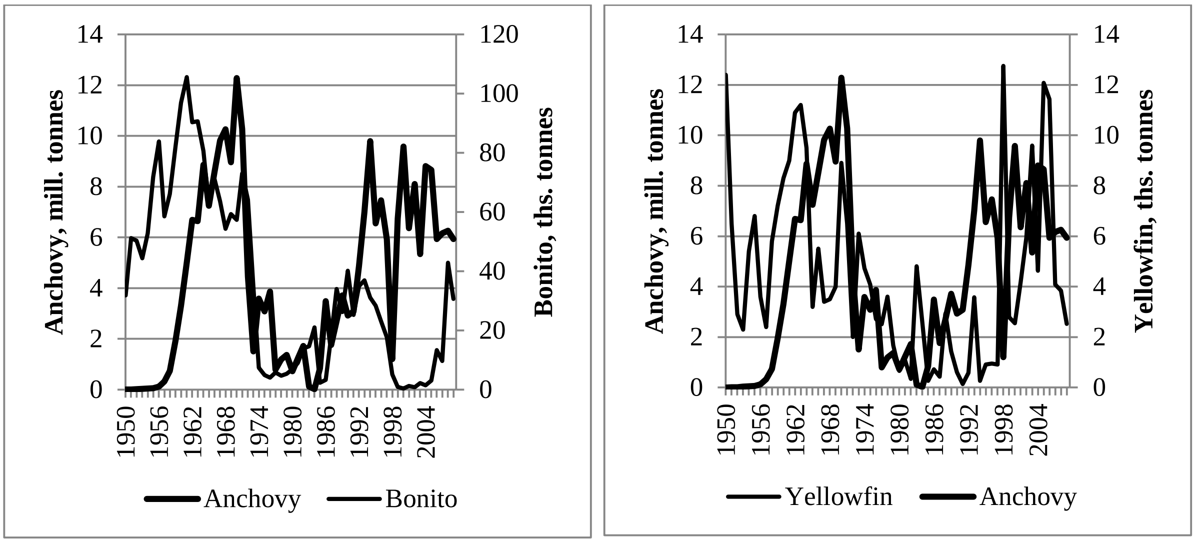
Anchovy, mill. tonnes
Bonito, ths. tonnes
14
12
10
8
6
4
2
0
120
100
80
60
40
20
0
1950
1956
1962
1968
1974
1980
1986
1992
1998
2004
Anchovy
Bonito
Anchovy, mill. tonnes
Yellowfin, ths. tonnes
14
12
10
8
6
4
2
0
14
12
10
8
6
4
2
0
1950
1956
1962
1968
1974
1980
1986
1992
1998
2004
Yellowfin
Anchovy

Figure 8

Figure captions

Figure 1

Landings of sardine predators in California and the sardine stock biomass 1932-2009. Sources: California fish landings data base (landings) and Kevin Hill (personal communication), Southwest Fisheries Science Center, La Jolla, California (sardine stock biomass). Sardine stock includes 0-age group.

Figure 2

Biomass of Pacific sardine, Northern anchovy, and Pacific mackerel. Sardine stock includes 0-age group, the others 1 year and older. Source: Pacific Fishery Management Council and Kevin Hill (personal communication), Southwest Fisheries Science Center, La Jolla, California (sardine stock biomass). Northern Anchovy biomass estimates for the years 1995-2009 are preliminary (Ben Fissel, personal communication).

Figure 3

Biomass of Pacific sardine and landings of five sardine predators. Source: Same as Figure 1.

Figure 4

Stock of Norwegian spring-spawning herring and catches of cod, haddock and saithe in the Barents Sea and the Norwegian Sea and at Iceland. Sources: (i) Herring stock 1950-1987: [10], (ii) herring stock 1988-2010: [11]; (iii) fish catches: International Council for the Exploration of the Sea (ICES).

Figure 5

Catches of pilchard and anchovy in South Africa and Namibia. Source: FAO Fishstat.

Figure 6

Catches of pilchard and three other species in South Africa and Namibia 1950-2009. Source: FAO Fishstat.

Figure 7

Peruvian catches of anchovy and sardine 1950-2009. Source: FAO Fishstat.

Figure 8

Peruvian catches of anchovy, bonito and yellowfin tuna 1950-2009. Source: FAO Fishstat.

Table 1

Sign of coefficient in a regression of predator landings on sardine biomass. * (**,***) denotes significance at the 5 (1, 0.1) percent level.

Positive	**Insignificant**	**Negative**
Barracuda***	California halibut	Albacore***
Bluefin***	Cabezon	Bonito***
Giant sea bass***	Hake	Butterfish***
Ocean whitefish***	Lobster	Jack mackerel***
Pacific halibut***		Ling cod***
		Market crab***
		Sablefish***
		Salmon**

Table 2

Sign of coefficient in a regression of landings of different fish species on landings of pilchard. * (**,***) denotes significance at the 5 (1, 0.1) percent level.

Positive	**Insignificant**	**Negative**
Rock lobster***	Panga seabream	Hake***
Chub mackerel***		Horse mackerel***
Unspecified marine fish***		Kingklip**
		Snoek*
		Herring$^{*a)}$

a) 1964-2009.

Table 3

Sign of coefficient in a regression of landings of different fish species in Peru on landings of anchovy 1960-2009. * (**,***) denotes significance at the 5 (1, 0.1) percent level.

Positive	**Insignificant**	**Negative**
Bonito**	Jack mackerel	Corvina drum*
Yellowfin*	Chub mackerel	Flatfishes**
	Groupers	Molluscs*
	Crabs	Mullets*
	Marine fish (unspecified)	Croaker**
	Menhaden	Smooth hounds*
	Sierra	Warehou**
	Rock seabass	
	Weakfish	
	Pompanos	
	Rays etc.	
	Sharks etc.[b)]	
	Skipjack tuna	
	Hake	
	Swordfish	

b) 1965-2009.