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The Role of Carrion Supply in the Abundance of Deep-Water Fish off California

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Abstract

Few time series of deep-sea systems exist from which the factors affecting abyssal fish populations can be evaluated. Previous analysis showed an increase in grenadier abundance, in the eastern North Pacific, which lagged epibenthic megafaunal abundance, mostly echinoderms, by 9–20 months. Subsequent diet studies suggested that carrion is the grenadier's most important food. Our goal was to evaluate if changes in carrion supply might drive the temporal changes in grenadier abundance. We analyzed a unique 17 year time series of abyssal grenadier abundance and size, collected at Station M (4100 m, 220 km offshore of Pt. Conception, California), and reaffirmed the increase in abundance and also showed an increase in mean size resulting in a ~6 fold change in grenadier biomass. We compared this data with abundance estimates for surface living nekton (pacific hake and jack mackerel) eaten by the grenadiers as carrion. A significant positive correlation between Pacific hake (but not jack mackerel) and grenadiers was found. Hake seasonally migrate to the waters offshore of California to spawn. They are the most abundant nekton species in the region and the target of the largest commercial fishery off the west coast. The correlation to grenadier abundance was strongest when using hake abundance metrics from the area within 100 nmi of Station M. No significant correlation between grenadier abundance and hake biomass for the entire California current region was found. Given the results and grenadier longevity, migration is likely responsible for the results and the location of hake spawning probably is more important than the size of the spawning stock in understanding the dynamics of abyssal grenadier populations. Our results suggest that some abyssal fishes' population dynamics are controlled by the flux of large particles of carrion. Climate and fishing pressures affecting epipelagic fish stocks could readily modulate deep-sea fish dynamics.

Introduction

Abyssal fishes live in the largest habitat on earth. Many are predators and scavengers [1,2,3,4] so they may substantially influence community dynamics across trophic levels over large areas of the planet. Top predators have been shown to alter the abundances and behaviors of their prey populations, exert selective pressures, alter biodiversity and alter biogeochemical cycling in both marine and terrestrial systems [5,6,7,8,9]. Much of our understanding of top down effects in ecosystems is derived from time-series of abundance and/or fishing data. The abundance or distributions of top predators in marine ecosystems also have been shown to be controlled by interannual scales of climate forcing such as El Nino and the PDO [10,11,12] and frequently long term reductions are observed as a consequence of fishing. Few time series of deep-sea systems exist from which the factors affecting abyssal fish populations can be evaluated.

A unique abyssal site, Station M, in the eastern North Pacific has been comprehensively studied over more than two decades [13,14]. The dynamics of life at the seafloor are strongly linked to the flux of particulate organic matter generated in surface waters. Seasonal and interannual increases in fluxes result in increases in sediment community activity and macrofaunal abundance, biomass, and average size and changes in the rank order of the most important taxa [15,16]. The larger epifaunal megafauna, principally echinoderms, show similar changes at interannual time scales, lagging the particulate flux by 11–22 months [17,18].

At Station M, abyssal fishes have been shown to increase three fold in abundance over a 15 year period [19]. The dominant fishes are two species of grenadier (Macrouridae), *Coryphaenoides armatus* and *C. yaquinae*, which comprise 97% of the fishes observed in camera sled transects and baited camera deployments. Their abundance was significantly correlated to that of the mobile epibenthic megafauna (mostly echinoderms) but not to surface climate indices used to predict production or to direct estimates of food supply, particulate organic carbon (POC) flux. Many grenadiers are slow growing and can reach ages of ~75 years [20,21]. Thus the changes in abundance that were observed almost certainly are driven mainly by migration in response to

variation in food availability. Indeed the abundance of epibenthic echinoderms was correlated to bentho-pelagic fish abundance [19]. However, later work by Drazen et al (2008), showed that the two fishes at this site eat very few echinoderms with as much as 69% of the diet of larger *C. armatus* composed of epipelagic carrion [1]. The carrion consisted of the remains of epipelagic fishes, principally jack mackerel and hake, and gonatid squids. The stomach content analysis was corroborated by stable isotope analysis of the grenadiers and their prey sources, again suggesting that carrion was the most important food type [1]. Fatty acid biomarker work examined the potential for the fishes to consume different prey and found that while carrion and benthic crustaceans were consumed that there was no evidence for substantial consumption of echinoderms, which had distinct fatty acid signatures [22].

Our goal was to evaluate if changes in carrion supply might drive the temporal changes in grenadier abundance at Station M. Several studies have indicated shifts in nekton abundance in the CA current system. For instance Zeidberg and Robison [23] showed the dramatic appearance of humboldt squid, *Dosidicus gigas*, off central California and persistence in the system from 2002 onwards. Brodeur et al [24] have shown regional shifts in the nekton community structure between 1998 and 2002 related to a shift in the sign of the Pacific Decadal Oscillation. We have analyzed a unique 17 year time series of abyssal grenadier abundance in conjunction with abundance estimates for surface living nekton eaten by the grenadiers as carrion. Our results show a positive correlation to Pacific hake, the most abundant nekton species in the region and the target of the largest commercial fishery off the west coast [25,26,27]. Our results suggest that, unlike other benthic community groups, some abyssal fishes' population dynamics are controlled by the flux of large particles of carrion.

Methods

Ethics Statement

The research conducted for this project was done in accordance with approved protocols (07–039) from the University of Hawaii, Institutional Animal Care and Use Committee.

Approach

To assess the relationship between carrion supply and grenadier abundance we correlated the grenadier time series to three metrics of nekton abundance. Direct estimates of standing stocks of carrion are not possible because the abyssal scavenging fauna rapidly removes this food from the seafloor [28,29] and visual observations are rare, even for large persistent carrion parcels such as dead whales [30,31,32]. We focused our attention on time series of abundance of nekton that were important carrion sources to the grenadiers as determined from diet studies [1]. These are gonatid squids, jack mackerel (*Trachurus symmetricus*) and Pacific hake (*Merluccius productus*). The latter makes up 61% of the pelagic fish biomass in the California Current ecosystem [26].

Grenadier data

Grenadier abundance was estimated using 54 towed camera transects from 1989 to 2007. The study area is known as Station M (34° 50′ N, 123° 00′ W), and consists of a 25×35 km area of the seafloor on the Monterey fan at 4100 m depth, 220 km offshore of Point Conception, California. [13,14] [34° 50′ N, 123° 00′ W; 13,14].

The camera system and the methods used to estimate fish density have already been described in detail elsewhere [19,33]. In short, the camera system was towed along the seafloor at an average speed of 0.8 m s^{-1} for a mean distance of 1254 m taking images every 4–5 s. The area viewed was the product of the distance of the transect and the effective transect width based on fish visibility across the transect axis [19], which varied between deployments due to lighting intensity and film development. Transects conducted within a month of each other (during the same field event) were considered replicates and density estimates were averaged. This yielded 39 time point estimates across the study period.

Size frequency distribution of the grenadiers was also determined. This was not possible using the towed camera because of the variable position and orientation of the fish above the seafloor. Downward looking baited cameras were used 10 times from 1990–1992 [34] and 3 times in 2005. In 2005 the "Sprint" video lander was used, recording 1 min video sequences with 4 min intervals between them. The characteristics of this lander have been described elsewhere [35], with the only modification being the removal of the electrical stimulation system so that fish could feed at the bait undisturbed. Fish total length was measured by taking individual frames from the video sequence and digitizing along the centre line of fish using Image J. From 1995–1998 grenadiers were captured during 8 sampling events using baited traps and longlines [36]. Fish total and pre-anal fin length were measured directly and their wet weight was estimated from existing length weight relationships for *Coryphaenoides* spp. In the NE Pacific [37]. Small grenadiers (<20 cm TL) are rarely observed at baited cameras [38]. So while the video lander, traps and longlines may not sample the entire grenadier size distribution, all of these sampling approaches were baited so they are internally consistent.

Nekton data

The California Cooperative Fisheries Investigation (CalCOFI) has conducted a comprehensive survey of fish larvae and eggs from the 1950's to the present day from Baja, California north to the US-Canadian border (http://calcofi.org/). Hake and jack mackerel eggs hatch in about one day of being spawned [39] so the local abundance of eggs will positively correlate with local spawning biomass of adults. Egg abundance is used to assess spawning stock biomass in fisheries assessments [40,41] including those for hakes [42,43,44]. There are no direct estimates of mortality during spawning for either hake or jack mackerel. In the absence of such data we must assume that mortality is constant over time for adult fish so that temporal variations in abundance of fish will be directly related to numbers of dying fish and sinking carcasses.

Several sampling types have been employed by the CalCOFI survey. Surface tows (Manta net) and vertical tows were excluded because hake and jack mackerel eggs were only identified and counted in these samples from 2006 to the present. An oblique bongo net system was used at all sampling stations and years and eggs were counted starting in 1988. This is a paired 71 cm diameter, 505 μm mesh net system. All tows were fished at 1–2 knots to 210 m depth. All data were standardized for the volume of water filtered. For squid, only *Loligo opalescens* paralarvae were counted. Gonatid squids brood their eggs in the meso and bathypelagic [45] thus their larvae are unlikely to appear in the CalCOFI samples and we could find no other alternative data sources with which to estimate their abundance off California.

The CalCOFI survey uses a regular suite of stations oriented in lines offshore in a southeasterly direction (330°) perpendicular to the California coastline. Lines are spaced 40 nmi apart in the offshore locations and stations are placed 20 to 40 nm apart along

each line. Since 1985 the CalCOFI program regularly sampled from line 76.7 off central California to line 93.3 at the US-Mexican border (Figure 1). Lines 60–73.3 were sampled in some years and we analyzed the data for this larger area as well. Stations are occupied on each line from the nearshore environment to offshore several hundred km. We examined all stations on these lines offshore of the relatively shallow basins in between the Channel Islands (stations 45 and higher). We also examined the egg time series for all sampling stations within 100 nmi or 1.5 degrees of Station M (lines 70–80 and stations 60–90). Surveys were conducted quarterly and all data were converted to a 13 month moving average of egg abundance (# 1000 m^{-3}) at each spatial scale.

The US National Marine Fisheries Service and Fisheries and Oceans Canada conduct annual stock assessments for pacific hake along the west coast of North America. This process synthesizes a considerable amount of data to generate models that estimate each year's total biomass and female spawning biomass among other variables [25]. Hake move offshore to spawn but the juveniles do not, so we used the female spawning stock biomass as the most appropriate index of potential carrion supply to grenadiers. The data we used were model median values.

Other time series of nekton abundance or community composition are available and have been summarized in Brodeur et al [46] based on coastal trawl and acoustic surveys. A pelagic trawl survey, focused on sampling young of the year rockfish, from Cape Mendocino south to San Diego covers the time period of interest [47]. However, it extends only 50 nmi offshore and data were for mobile 1 year old hake (no data for jack mackerel), thus the CalCOFI data seemed a better source of information. There is also a biennial acoustic survey along the US West coast to survey

hake biomass [48]. Sampling is during the summer when the adults are feeding at the shelf break. The survey covers from Queen Charlotte Sound, Canada to 35.7° N (just north of Station M) and from the 50 m to the 1500 m isobath in transects every ~20 km latitudinally (Fleischer et al 2005). So this time series does not characterize the hake population when it could be available to abyssal scavengers. Furthermore, during the survey season few hake are reported south of San Francisco. Due to the characteristics of these surveys they were not used to evaluate temporal patterns in nekton communities near Station M.

Data analysis

Correlations were performed between grenadier and nekton egg monthly abundance using 13 month centered moving averages from the time series because they were discontinuous. Correlations with time lags of −12 to +12 months were used. Yearly estimates of hake female spawning stock biomass were also correlated to yearly averages of grenadier abundance. In this case no time lags were used because of the broad temporal scale of the measurements. To correct for serial autocorrelation the modified Chelton method was used [49]. Tests were considered significant if $p < 0.05$. All statistical analysis was conducted using Statistica 7.1 software (Statsoft Inc., www.statsoft.com).

Results

In addition to previously documented increases in the abundance of grenadiers at Sta. M. [19], we show that their average size has increased compared to the earliest portion of the time series (ANOVA, $F_{2,473} = 52$, $p < 0.001$, Figure 2). 197 fish measured in baited camera deployments from 1990–1992 had a
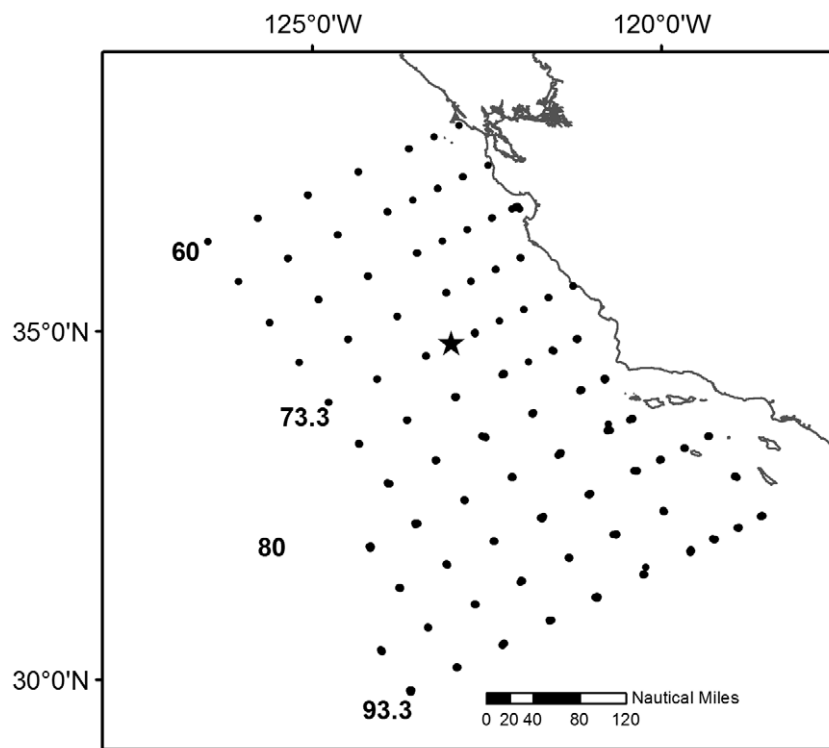

Figure 1. Stations used for analysis from the California Cooperative Fisheries Investigation (CalCOFI) fish egg surveys. The California coastline is depicted from San Diego in the south to San Francisco to the north. Several of the sampling line numbers are shown for reference. Station M is shown by the star.
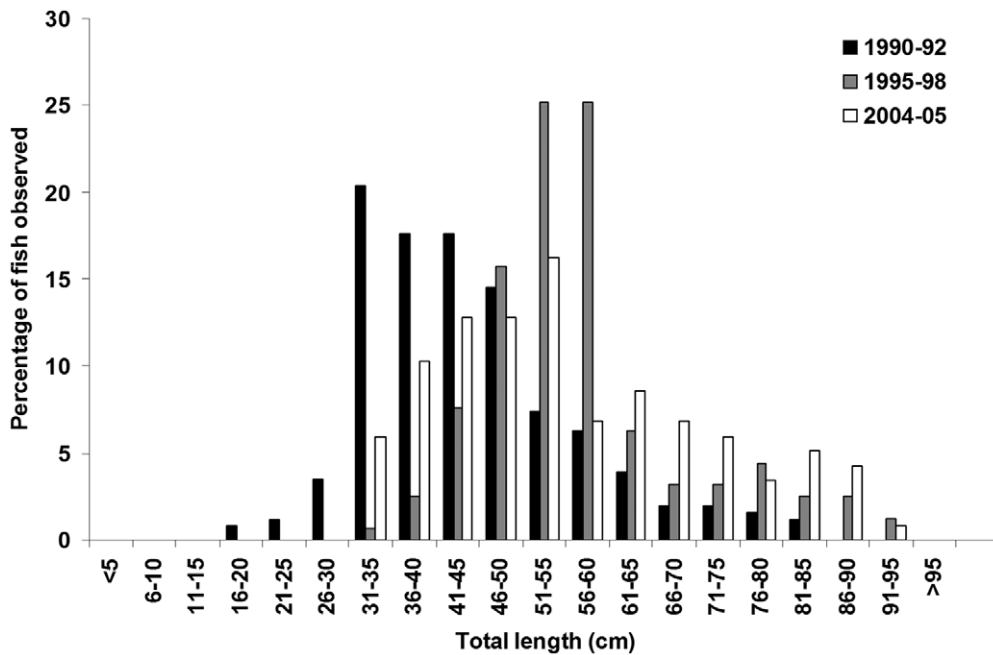doi:10.1371/journal.pone.0049332.g001

Figure 2. Size frequency distributions of *Coryphaenoides* spp. showing an increase in mean size from 1990–92 to 2004–2005.
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mean total length (TL) of 46 cm. 159 fish measured from 1995–1998 had a mean TL of 59 cm similar to that measured from 2004–2005 (55 cm, 117 fish). This change in length from the first period to the last two is a change in mean mass of 0.4 to >0.8 kg based on length-weight relationships [37].

Significant correlations between grenadier abundance and hake but not jack mackerel egg abundances were found (Figures 3 and 4). Grenadier abundance was negatively correlated with jack mackerel egg abundance over most of the time lags but not significantly so. In contrast, hake egg abundance was positively correlated with grenadier abundance at all spatial scales and stronger at the smaller 100 nmi spatial scale (Figure 4). At the larger spatial scales significant correlations (p<0.05) occurred when hake egg abundance led grenadier abundance by 0–5 months. At the smaller 100 nmi scale correlations were significant from +6 to −7 months. These correlations are influenced strongly by the coincidence in peak years (2001–2002) later in the time series though at the 100 nmi scale the fluctuations in both grenadier and hake egg density are also significantly correlated during the early to mid 1990′s (Figure 3).

Correlations between yearly estimates of hake female spawning stock biomass along the west coast of the North America and grenadier abundance at Station M towards the southern extent of the hake stock were not significant. Although when grenadier abundance rose at Sta. M in the early 2000′s, hake biomass rose concurrently (Figure 5).

Discussion

The changes in grenadier population structure followed metrics for hake biomass, suggesting that these abyssal fishes respond rapidly to changes in epipelagic carrion sources. Rapid consumption once carrion reaches the seafloor [29,30,31] may explain the small temporal lags (Figure 4) between the abyssal and epipelagic fish populations at Sta. M. In contrast to the results for hake, correlations to jack mackerel egg density were negative and insignificant (Fig. 3). This species has much less biomass in the

Figure 3. Time series of grenadier and epipelagic nekton egg abundances. Grenadier abundance (thick black line) and (a) hake and (b) jack mackerel egg abundance for the larger sampled area (gray dots), the annually sampled region (thin gray line) and only stations within 100 nmi of Station M (thick gray lines) are shown.
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California Current ecosystem compared to hake [46] and is widely distributed without a pronounced spawning period [50,51,52] which may explain the difference.

Our results show that there was both an increase in abundance of grenadiers and an increase in mean size such that fish biomass

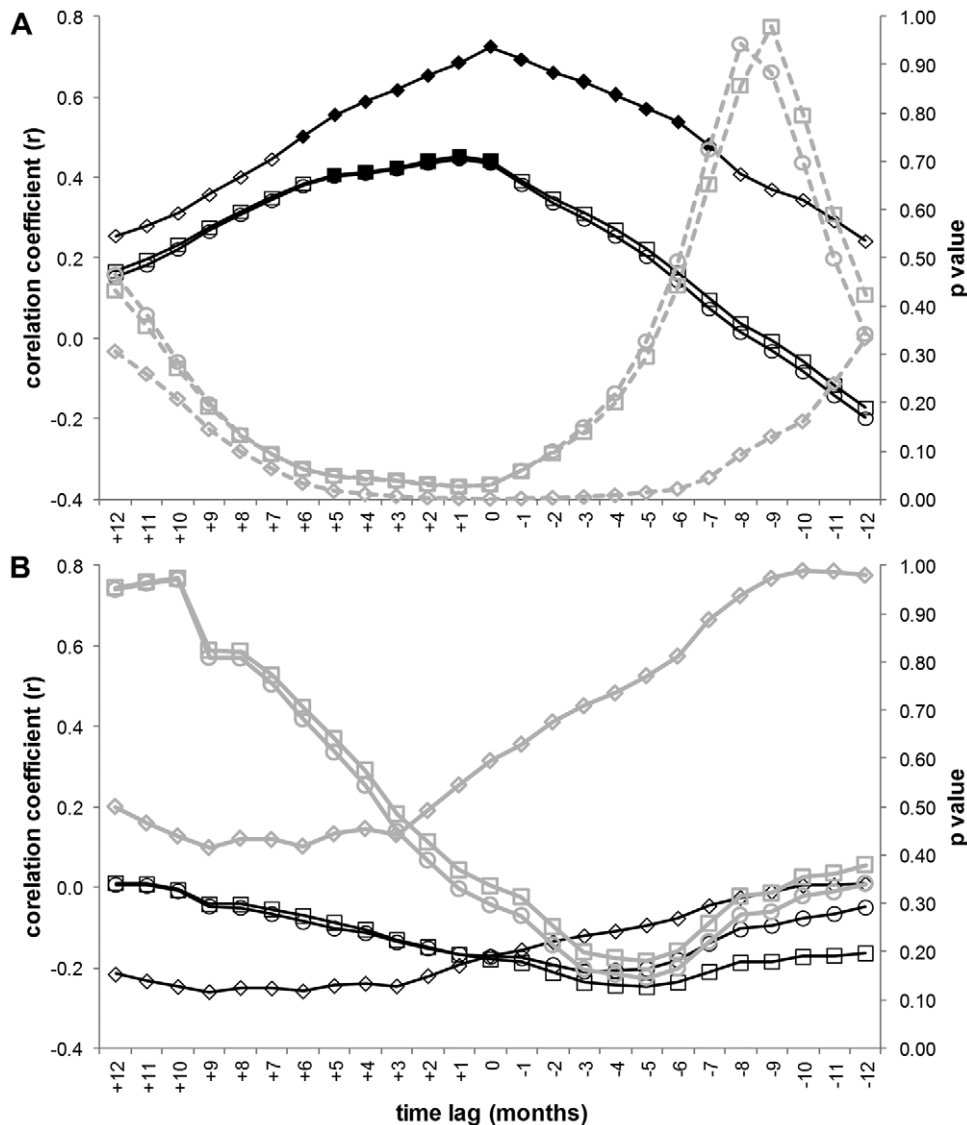**Figure 4. Correlation coefficients (black) and associate p values (grey) between grenadier and nekton egg abundances.** Correlations were lagged from +12 (eggs leading grenadiers) and −12 (grenadiers leading eggs) months. Correlations to hake (A) and jack mackerel (B) from the 100 nmi (diamonds), regularly sampled area (circles) and larger area (squares) are shown. Solid black symbols for correlation coefficients indicate a significant correlation (p<0.05 as shown by the corresponding grey symbols).
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at Station M increased ~6 fold. Almost certainly the changes are the result of migration rather than local individual and population growth because of the slow growth rates of grenadiers [von Bertalanfy k = 0.02–0.11 and longevity 25–73 years; 20,21,53]. Migration rates of 250 km month^{-1} are possible given grenadiers slow (~0.1 m s^{-1}) continuous swimming [54,55]. Studies of abyssal grenadiers in the North Atlantic and in the central North Pacific gyre also observed seasonal or interannual changes in lengths attributing them to migration rather than local population effects [56,57].

While migration is the most likely explanation for the current results, grenadier reproduction and/or recruitment variation is an alternative explanation. Increases in the mean size of grenadiers and the absence of the smallest individuals (Figure 2) in the latter sampling periods could be explained by a recruitment pulse which then moved through the population, perhaps affecting abundance patterns as well. It has been suggested that deep-sea fishes [58] and

other animals [17] have sporadic recruitment events. However, this is unlikely in the case of the grenadiers at Sta. M for several reasons. The changes in size that were observed are not monotonic with time. The mean size peaked in the 1995–1998 sample (Figure 2). Also, the change in size likely represents a longer duration of growth than the time elapsed. There are no validated age and growth estimates for *C. armatus*, however, we do know that other related species in the genus grow very slowly. A recruitment pulse is also unlikely because the expectation would be an increase in mean size over time as a good year class moves through the population but the abundance would also be expected to decline through natural mortality. A recruitment pulse is also unlikely to explain our results given the apparently localised area where the correlation to hake egg abundance was significant.

The location of hake spawning probably is more important than the size of the spawning stock in understanding the dynamics of abyssal grenadier populations. The correlation to hake egg density
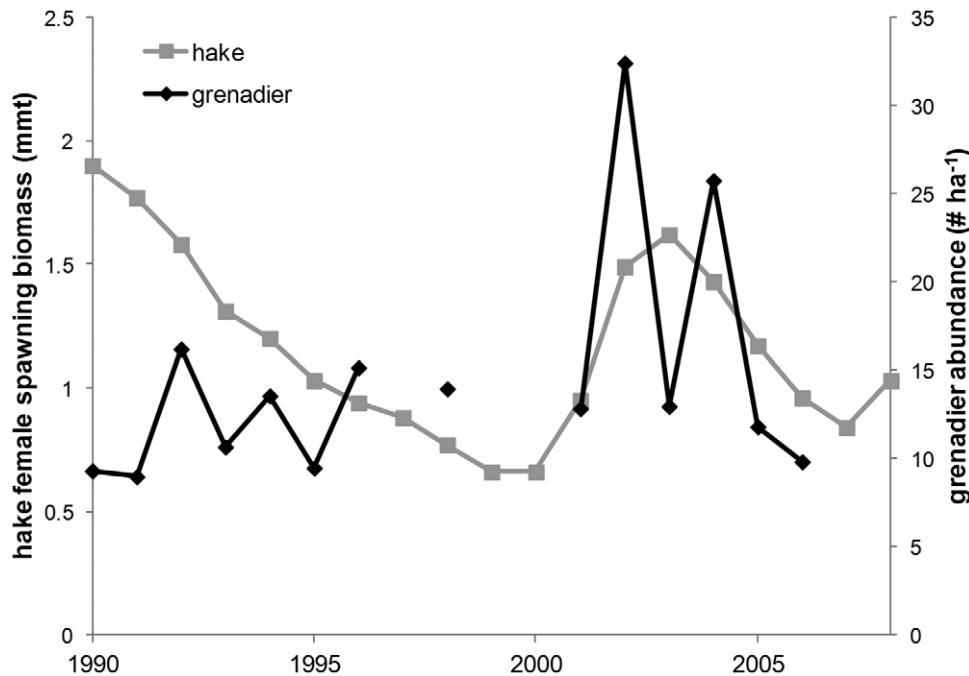
Figure 5. Time series of yearly spawning stock biomass of hake [25] and yearly mean grenadier abundance at Sta. M.
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is stronger for data from a more localized region (100 nmi), probably because carrion rapidly settles to the seafloor. Close spatial coupling is also supported by the finding that hake spawning stock biomass for the whole California Current system showed no significant relationship to grenadier abundance. Hake spawn principally off central and southern California but can extend off shore of Baja California, Mexico and as far north as Oregon [26,27,59]. The CalCOFI data set's regular sampling grid only covers the middle of this range limiting our ability to quantify variations in spawning location. However, coastal trawl and acoustic surveys provide a qualitative comparison to the grenadier data. They inferred more spawning activity north of California in the late 1990 s from the presence of pre-recruits and observed a southern shift in the early 2000′s due to a cold water La Nina event [25,27]. This broad pattern is coincident with the increase in grenadier abundance at Station M. In spring and summer, hake move inshore and north to feed and a recent study has shown that the extent of these movements is affected interannually by variation in along-slope California undercurrent flow [26]. Thus it is interesting to speculate that the grenadiers might show a similar migration pattern on annual or interannual timescales. Not all peaks in hake egg density correspond to a peak in grenadier abundance at Sta. M suggesting other factors are also important. It may be that the pattern we see at Sta. M is part of a larger heterogenous and changing distribution of grenadiers on the abyssal floor which is imperfectly captured at our single study location.

A growing body of literature is illustrating the ways in which climate, surface productivity and export flux control abyssal ecosystem function [16,17,60,61]. For the grenadiers, these indices do not correlate to their population dynamics but proxies for carrion flux and epibenthic megafaunal abundance both do [19]. The correlations between grenadier and megafaunal abundance were lagged by 9–20 months, whereas correlations between grenadier and hake showed lags of less than ~6 months, suggesting that the grenadiers respond first to trophically more

important carrion [1,22]. This implies that a full understanding of abyssal ecosystem dynamics needs to incorporate knowledge of epipelagic nekton as well as primary producers.

Climate and fishing pressures could modulate deep-sea fish dynamics. Climate change induced surface warming may reduce epipelagic nekton biomass but due to their mobility can also cause shifts in their distributions and changes in community composition [23,46,62,63]. Studies have suggested that fish will move north [62] and closer to the coast [46,63] as low productivity regions expand in the gyres. *C. yaquinae* is limited to the North Pacific central gyre at depths deeper than 4000 m and may not be able to follow [64]. *C. armatus* is found shallower, up to ~3000 m and worldwide [57], so might be less limited in its movement ability. Fishing activities in surface waters likely have little influence on vertical small particle flux and thus on most of the abyssal benthic community but our results suggest they could affect deep-sea scavengers, greatly extending the area and vertical extent of fishing influence. In the short term, fishing can increase carrion flux as a result of discarded bycatch [65,66]. Fisheries offal has been noted in the stomachs of deep-sea fishes [67,68]. In the long term, global reductions in fish stocks [69] should reduce carrion flux [70]. Decreases in whale carrion flux from commercial whaling in the 20th century may have caused extinctions of endemic whale fall invertebrates [71]. However, in the Atlantic, while Bailey et al [72] showed changes in fish abundance below the depths reached by fishing boats, known scavengers were no more likely to change in abundance than non-scavengers.

Other species of deep-sea fish could be influenced by the dynamics of epipelagic fish stocks because many feed on carrion [67,73,74,75,76,77,78,79,80] or are strongly attracted to bait [29,30,38,55,81,82,83,84,85,86,87,88]. Many of these fishes live in areas where there are seasonal variations in abundance of epipelagic species due to migration (i.e. albacore [89] or whales [32]) or spawning aggregations (i.e. blue whiting or hoki [90,91]). Future studies of the deep-sea ecosystem should incorporate an understanding of the status and trends of nekton populations.

Although time series of abyssal fish populations are rare [the only other is in the North Atlantic; 72], there is more data for the continental slopes. These systems are directly affected by fisheries complicating interpretation of population changes but opportunities exist to evaluate how pelagic fish dynamics effect deep-sea demersal fish populations.

Acknowledgments

Author Contributions

Conceived and designed the experiments: JCD DMB HAR KLS. Performed the experiments: DMB HAR KLS. Analyzed the data: JCD DMB. Contributed reagents/materials/analysis tools: JCD DMB HAR KLS. Wrote the paper: JCD DMB HAR KLS.

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