Temporal and spatial patterns in the abundance of jellyfish in the northern Benguela upwelling ecosystem and their link to thwarted pelagic fishery recovery

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There has been debate in the literature about whether jellyfish abundance has increased in the northern Benguela upwelling system, or not, over the past five decades and what impact they are having on pelagic fish. Here we review old expedition literature as well as more recent spatial and temporal patterns in distribution of jellyfish off Namibia at a number of different scales, using both published and previously unpublished data. Specifically, we have used data from fishery-dependent sources of both the demersal (359 638 trawls) and pelagic fisheries (11 324 purse-seine sets) that cover the period 1992–2006, supported by data from fishery-independent demersal (6 109 trawls) and pelagic trawls (1 817 trawls) from 1996 to 2006. Using frequency of capture as an index of abundance, it is clear that jellyfish are not randomly distributed within the northern Benguela ecosystem, but show specific areas of concentration that broadly reflect regional oceanography and the distribution of other zooplankton. Although jellyfish are present throughout the year, peaks in abundance are shown that often coincide with peaks in the spawning activity of fish of commercial importance. Interannual changes in jellyfish abundance observed from all sources do not agree, with some showing increases, others declines, and still others showing no change, which suggests caution should be exercised in their interpretation. Based on the multiple lines of evidence synthesised here, we conclude that jellyfish abundance has increased concomitant with a decline of pelagic fish stocks. We conclude that future recovery of the pelagic fishery off Namibia is likely to be considerably challenged because of significant overlaps in space and time between fish and jellyfish, and through the effects of competition and predation effects of jellyfish on fish.

Keywords: Aequorea, Chrysaora, fish recruitment, jellyfish joyride, overfishing

Introduction

Scyphozoans and other jellyfish often display pronounced fluctuations in population size (Mills 2001) that can have substantial socio-economic consequences. Jellyfish can reach naturally high densities in enclosed embayments and at physical oceanographic discontinuities such as fronts (Graham et al. 2001). Some of these population fluctuations are strongly seasonal in nature, reflecting life-cycle characteristics of the species involved, and peaks in abundance are mirrored by seasonal changes to the structure of marine plankton communities (Feigenbaum and Kelly 1984). However, there is growing evidence to suggest that ‘blooms’ of some species are occurring more frequently and for longer periods in recent years, perhaps in response to the altered functioning of marine ecosystems (Mills 2001, Purcell et al. 2007, Richardson et al. 2009, Brotz et al. in press). A number of anthropogenic factors have been implicated in these increases, and it is likely that these act synergistically (Purcell et al. 2007, Richardson et al. 2009). These factors include overfishing, eutrophication, climate change, and a proliferation of hard substrata (Purcell et al. 2007, Richardson et al. 2009), and may involve recently introduced species (Graham and Bayha 2007, Oguz et al. 2008). Jellyfish blooms can negatively affect regional economies through lower fishery (J Quiñones, Instituto del Mar del Perú, Instituto del Mar del Perú, ...)
Large blooms of jellyfish are not confined to coastal embayments, however, as seen over the continental shelf off Namibia in 2003 when the biomass of these organisms was considered to exceed that of fish by a factor of four (Lynam et al. 2006). It is thought that overfishing in the early 1970s was probably responsible for these changes (Bakun and Weeks 2006), although subsequent environmental anomalies (Shannon et al. 1986, Boyd et al. 1987, Gammelsrød et al. 1998, Mohrholz et al. 2004, Bartholomae and van der Plas 2007, Rouault et al. 2007) may have advantaged jellyfish. Shelf waters off Namibia are subject to coastal upwelling, and pelagic fish communities were dominated by sardine Sardinops sagax and anchovy Engraulis encrasicolis prior to the mid-1970s. These small pelagic fish are considered wasp-waist species (Cury et al. 2000) that use the high primary production relatively efficiently, and they were subject to industrial fisheries that date back to the mid-20th century (Boyer et al. 2000). Annual sardine catches were around 200 000 tonnes for much of the 1950s (Le Clus et al. 1987), then increased throughout the 1960s to more than 1.5 million tonnes in 1968 after good recruitment in the late 1950s and early 1960s (reviewed by Cury and Shannon 2004). Following heavy fishing throughout the 1960s, sardine stocks suffered several crashes (Heymans et al. 2004), from which heavy fishing throughout the 1960s, sardine stocks

1960s (reviewed by Cury and Shannon 2004). Following heavy fishing throughout the 1960s, sardine stocks suffered several crashes (Heymans et al. 2004), from which they have failed to recover (Boyer et al. 2001, Boyer and Hampton 2001). Interestingly, and unlike many other coastal upwelling systems (Chavez et al. 2003, Bakun and Weeks 2008), there has been no regime shift between sardine and anchovy off Namibia (Cury et al. 2000, Cury and Shannon 2004). This is perhaps in part because the system has always been considered a sardine-dominated one, even in pre-industrial times (Shackleton 1987) and in part because anchovy, the possible replacement species, was also subject to heavy exploitation (Butterworth 1983). Instead, a number of opportunistic species including horse mackerel Trachurus capensis, the bearded goby Sufflogobius bibarbatus and jellyfish have replaced the dominant species (Cury and Shannon 2004).

While there are robust data detailing the collapse of pelagic finfish populations in Namibian waters (e.g. Boyer and Hampton 2001), there is no similarly reliable time-series for jellyfish, so evidence for their increase is currently anecdotal. It should be noted that we interpret ‘jellyfish’ here in terms of Chrysaora fulgida and Aequorea forskalea, which have been recognised as the dominant taxa in the region (Lynam et al. 2006). Although the two species belong to different cnidarian classes, both have metagenic life cycles and attain a relatively large size (A. forskalea, 12 cm central disk diameter; C. fulgida, >80 cm diameter; Buecher et al. 2001) and could be caught by the mesh sizes examined in this study. The absence of robust jellyfish data, and the lack of available staff and the appropriate infrastructure in Namibia to study jellyfish (as they have no commercial value), has meant that our present understanding of them is limited. Knowledge has been derived piece-meal from imperfect (e.g. Fearon et al. 1992; vertical Bongo nets cannot be used to quantitatively determine the abundance or distribution of large medusae), once-off (Brierley et al. 2001, 2004, 2005, Buecher et al. 2001, Sparks et al. 2001, Lynam et al. 2006) or incomplete (Venter 1988: monthly only from March to September) datasets. This in turn means that our knowledge resembles a mosaic in which most of the pieces are missing. Here we attempt to consolidate the published material incorporating data that have been collected but not yet synthesised and interpreted. Our intention is to understand the abundance and distribution of jellyfish in space and time, and assess their implications for fisheries off Namibia.

**Material and methods**

We used two primary data sources: viz. fishery-dependent data and fishery-independent surveys.

**Fishery-dependent data**

Two sources of fishery-dependent data, from the pelagic and demersal sectors, were used to explore patterns in the relative abundance of large jellyfish off Namibia. When interpreting jellyfish data from commercial fisheries, there are a number of temporal and spatial biases associated with the targeting of particular fish species that need to be considered.

Commercial pelagic data were obtained from the pelagic database (housed and controlled by National Marine Information and Research Centre, NatMIRC) that records catch and landings information from the purse-seine vessels. These target sardine and juvenile horse mackerel, although anchovy, round herring Etrumeus whiteheadi and sardinella Sardinella australis are also caught when available. The fishing season starts in January north of Walvis Bay targeting juvenile horse mackerel, round herring and anchovy for fishmeal production. Of these, only horse mackerel is managed by quotas. Later in the season (usually around March/April), the fishery targets the more valuable sardine, mainly for canning. Normally, the sardine season is from March/April to September. The number of months that fishing takes place is limited by the time it takes to fill the total allowable catch for sardine and horse mackerel, which have been low in recent years. The preferred fishing area is close to Walvis Bay harbour (23° S), but purse-seiners may fish up to the border with Angola (17°15’S: and in some years even farther north) and south to near Luderitz (25° S) (Figure 1b). There are no restrictions on where purse-seiners are permitted to fish (but outside the marine protected area in the south since 2008/2009), and most fish are normally caught inshore of the 100 m isobath. Since Namibia’s independence in 1990, the number of licensed vessels has generally declined, with a maximum of 43 in 1994, subsequently decreasing to 9 or less vessels in recent years. Nets used since 1990 have a mesh size of 27 mm for sardine and 12.8 mm for anchovy. All purse-seiners presently have observers onboard who, in collaboration with the skippers, fill out logsheets that include the position of sets and the estimated size of the catch, although few vessels were staffed in the early 1990s. Species other than small pelagic fish are usually noted as ‘other’. The abundance of jellyfish is often substantially under-reported in the commercial data, because jellyfish are sometimes...
not pumped into the vessel as they block the refrigerated seawater system used to keep the fish cold. Fish catches are landed in the harbours at Walvis Bay and Lüderitz, where inspectors calculate the landings per species, if the condition of the fish allows. Inspectors then collect sub-samples of the catches for scientists, but as the boats may land several sets made in different locations, the exact position of the catches cannot always be determined. Further details of the methods used by the pelagic fishing fleet can be found in Boyer et al. (2001), and a history of the fishery is described in Schülein (1978), Butterworth (1983), Thomas (1986), Le Clus et al. (1987) and Crawford et al. (1987). Information on jellyfish catches used here originates from the landings data (A-forms) from Walvis Bay Harbour and spans the years 1992–2006. Jellyfish data used are expressed as (percentage) frequency of occurrence in inspected samples \( (n = 11,324) \) by month and year of collection. Different species of jellyfish were not identified, so all jellyfish have been considered together.

Although jellyfish are primarily pelagic organisms, they can also be caught by demersal trawl nets during lowered to the bottom or hauling to the surface. We used commercial data from trawl vessels that target hake *Merluccius capensis* and *M. paradoxus* and monkfish *Lophius vomerinus*. These species are fished throughout the year and throughout the Namibian Exclusive Economic Zone, except waters <200 m depth (and since 2006, at water <300 m depth south of 25°S) and so might be less biased temporally than the pelagic data (see summary of biases in Table 1). The total number of vessels has fluctuated since 1990, but generally decreased from about 140 vessels in 2004 to 100 in 2007. As part of the management measures in the demersal sector, nets used since 1990 have minimum mesh sizes of 110 mm for hake and 75 mm for monkfish; the history of the fishery is detailed in van der Westhuizen (2001). As in the purse-seine fleet, all vessels are obliged to host observers onboard, and to carry logbooks onboard in which officers fill in daily logsheets of fishing activities. Data from these logsheets are later entered into the database of the Ministry of Fisheries and Marine Resources (MFMR), from which the present data were extracted (Figure 1c). Jellyfish data used here span the period 1997–2006, and are expressed as (percentage) frequency of occurrence in trawls \( (n = 359,638) \) geo-referenced by latitude (in 1° bins) and bathymetry (in 50 m depth bins), month and year of collection. As in the pelagic dataset, the different species were not identified and all jellyfish have been considered together.

**Fishery-independent data**

Although a number of data sources are available, we have focused on the pelagic and demersal data collected by the *RV Dr Fridtjof Nansen* over the period 1994–2006 as they represent the most comprehensive, consistent, inclusive and synthesised data available. Additional to the time-series
data, those from experimental regional surveys with the RV Dr Fridtjof Nansen that cover the Namibian continental shelf in the period 2000–2006 have been incorporated. Catch data were segregated by year and survey type (pelagic/demersal), and a brief overview of each is provided below.

Two different-sized pelagic sampling trawls (modified Åkrahamn trawls, Valdemersen and Misund 1994) were used to sample the water column for verification of acoustic targets, the smallest with a vertical opening of about 12–15 m and the bigger one with an opening of 15–18 m. Both had codends with 16 mm mesh. During some experimental surveys, pelagic trawls were fitted with a multisampler remotely opening and closing three separate codends that allowed for depth-stratified sampling (Engås et al. 1997). For all tows, the standard tow time was about 30 minutes, although occasionally shortened in cases of large catches. Tow speed was standardised at approximately 3.5 knots (1.8 m s⁻¹). The gears deployed and the fishing methods by the RV Dr Fridtjof Nansen are detailed in Sætersdal et al. (1999).

All demersal catches were made using a standard Gisund Super Bottom sampling trawl. The wing tip-to-wing tip distance of this trawl is 21 m, corresponding to an effective horizontal opening estimated at 18.5 m when taking into account herding and avoidance effects (Strømme and Ilende 2001). The horizontal spread of the trawl is kept fairly stable across all depths, corresponding to a door spread distance of 45–55 m, by the use of a 9.5 m restrainer rope between the warps mounted about 150 m from the doors. The vertical net opening of the trawl is monitored by means of Scanmar sensors and is nominally between 4.5 m and 6.0 m. The codend has 20 mm mesh, and is fitted with an inner net of 10 mm mesh.

Although the entire catch was sampled by species on retrieval, jellyfish data are expressed here as (percentage) frequency of occurrence by month, year, latitude (in 1° bins) and bathymetry (in 50 m depth bins). The reason for using frequency of occurrence/capture, as opposed to biomass or abundance, reflects biases in the dataset (see Discussion, Table 1), as well as differences in the gear-types employed and their ability to retain sampled jellyfish. Although different species of jellyfish were identified in some surveys, this was not consistent across time, and so all jellyfish species have been combined for robustness and to ensure the analyses are comparable to those of the fishery-dependent data. Data from 1 817 pelagic and 6 109 demersal trawls have been used (Figure 1d).

Unlike the other datasets employed here, information on the vertical distribution of jellyfish could only be obtained from the fishery-independent, dedicated surveys on board the RV Dr Fridtjof Nansen (September 1999, September 2001, August 2003). Results of the former two surveys have been published and detailed methods were described in Brierley et al. (2001), Buecher et al. (2001) and Sparks et al. (2001) for the 1999 survey and in Brierley et al. (2004, 2005) for the 2001 survey. Here we report on the data collected during the 2003 survey, and previously commented upon (in part) by Lynam et al. (2006). In summary, the water column was sampled for jellyfish at an inshore and an offshore station off Walvis Bay during August 2003 throughout the day–night period using a series of stratified pelagic hauls. Jellyfish catches in each net were standardised per unit volume fished and the proportional distribution of jellyfish throughout the water column was determined. Profiles were then averaged across locations by day or night for comparative purposes.

**Biases in jellyfish data**

As detailed above, the new data used here to explore patterns in the relative abundance and distribution of
The former datasets are extensive but have a level of bias, data obtained from regional research surveys and cruises. Trawl and purse-seine fisheries and fishery-independent catch is individually based, so that contamination of a trawl reflected in the landings.

We have used data from both demersal and pelagic trawls, even though jellyfish are primarily pelagic and not demersal organisms, to try and minimise biases in the different datasets engendered by skippers’ perceptions about jellyfish and the fate of the catch. Purse-seine skippers avoid areas where jellyfish are visible due to value loss of the catch and mechanical problems to the cooling system. Pelagic fishers also tend to target dense shoals of fish that might avoid high concentrations of jellyfish, so contamination with the latter probably only occurs in those nets that are set in an area of several small shoals with jellyfish between them. On capture, small pelagic fish are processed in bulk and are either destined for cans (high value) or are reduced to fishmeal (low value), and a skipper is unlikely to set a net if there is a risk of major catch contamination by jellyfish. Pelagic fishers will therefore generally not set nets whenever concentrations of jellyfish are visible at the surface, and so trends in jellyfish abundance observed from the pelagic fishery may not necessarily, or only in part, be reflected in the landings.

By contrast, the processing of the majority of a demersal catch is individually based, so that contamination of a trawl by some jellyfish carries lesser financial penalties, and a skipper’s decision-threshold is likely to be lower than that of a pelagic fisher. Further, the demersal trawl nets are generally towed quite rapidly to the surface, being partly closed, and it is therefore unlikely that large quantities of jellyfish would be caught in the pelagic zone. As a consequence, while we anticipate that the frequency of jellyfish capture in demersal fishing operations will be lower than that from the pelagic fishery, the data collected are more ‘random’, and may perhaps be more representative: the low frequency of occurrence being compensated for by the very large number of samples collected.

**Statistical analyses**

To examine the relative performance of the four datasets used here (fishery-dependent, fishery-independent; pelagic, demersal), we have compared the monthly average frequency of jellyfish occurrence (by year). A two-way factorial ANOVA was performed with dataset and trawl type as predictors. Data were log transformed, and visually inspected for normality and homogeneity of variance.

To identify relationships between jellyfish and a suite of predictors, we used a generalised additive modelling (GAM) approach (Hastie and Tibshirani 1990). The response was the proportion of trawls that had jellyfish present, which is used here as an index of relative abundance. Predictors used in our models included temporal (Year, Month) and spatial (Bottom depth, Latitude) terms. The predictor Year provides a time-series of jellyfish abundance adjusted for all predictors in the model. The Month effect reflects the seasonal cycle in jellyfish abundance; Latitude represents jellyfish distribution along the north–south oriented coastline in Namibia; and Depth captures the cross-shelf changes in jellyfish abundance.

We used a binomial error structure and the logit link function to account for the bounded (between 0 and 1) response variable and the non-normal error structure. Plots of model residuals showed they were relatively well behaved. GAMs were fitted using the mgcv (mg cross validation) package in R, where smooth terms are represented using penalised regression splines with smoothing parameters selected by restricted maximum likelihood (REML) (Wood 2006).

Only data within Namibian waters to 1 000 m water depth were included in the analysis. Data before 1996 from the RV Dr Fridtjof Nansen were excluded because jellyfish were not recorded (see Table 2).

**Results**

Table 2 summarises the data and is presented (as monthly averages by year) to show variations in the frequency with which jellyfish were recorded in the different datasets; a description of the data as they pertain to interannual patterns is presented below. Overall, jellyfish were recorded significantly less frequently in the demersal than pelagic datasets (ANOVA, df = 1, \( F = 39.909, p < 0.001 \)), and were less commonly recorded in the fishery-dependent than independent datasets (ANOVA, df = 1, \( F = 53.109, p < 0.001 \)). The interaction term was similarly significant (ANOVA, df = 1, \( F = 33.893, p < 0.001 \)).

**Latitude**

Jellyfish are found along the entire length of the Namibian coast (Figure 1). Results from the GAM of the fishery-dependent demersal data (Figure 2c) indicate, however, that jellyfish tend to be significantly more commonly encountered in the region 20°–24° S (central Namibia) than elsewhere. Similar results were obtained from the GAM of the fishery-independent demersal data (Figure 2a), but not the fishery-independent pelagic data (Figure 2b). All three datasets that had latitudinal data indicated that jellyfish were caught much less frequently in the southern part of the region than elsewhere.

**Cross-shelf**

There is a strong cross-shelf decline in the abundance of jellyfish off Namibia evident in all three datasets with depth-resolved data (Figure 2). Jellyfish are most prevalent in waters <300 m depth and decline rapidly in deeper waters, before increasing again slightly at depths greater than 600 m.

**Seasonal**

Jellyfish are present off Namibia throughout the year (Figure 2). Both the fishery-independent datasets suggest a summer peak in jellyfish abundance, with the benthic data indicating an additional winter–spring peak, although the seasonal effect in both models has large standard errors and thus should be interpreted with some caution (Figure 2b). The two commercial datasets have a marked winter and early spring peak (Figure 2). Overall, there appears to be most evidence for a winter–spring peak from the current data.
Table 2: Interannual changes in the average monthly frequency of occurrence (%) of jellyfish in trawl catches off the Namibian coast 1990–2006, by gear type (pelagic or demersal) and dataset (fishery-dependent, fishery-independent). Also shown are the total number of trawls per year (N_{samp}) and the number of months (N_{mo}) sampled.

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<th>Year</th>
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**Interannual**

There was no agreement among the different datasets regarding interannual changes in the frequency of jellyfish catches over the time period examined here. The fishery-dependent demersal and pelagic datasets suggest (respectively) that jellyfish populations have either been declining steadily since 1996 (Figure 2c), else they are fluctuating (Figure 2d). For the fishery-independent data, the demersal data suggest that there has been a marked increase in the frequency with which jellyfish have been caught off Namibia since the start of the time-series (Figure 2a), whereas the pelagic data (Figure 2b) suggest there has been a gradual decline (note here that reporting levels of jellyfish were very low prior to 1995 [see Table 1], and so analyses are restricted to the period post-1996).

**Water column**

Data presented here from an inshore and offshore station off Walvis Bay show that whereas jellyfish can be found throughout the water column to a depth of 80 m, the bulk of the population is centered in near-surface waters (Figure 3). There is no clear evidence that either species displays diel vertical migration (DVM) at the population level (Figure 3).

**Discussion**

**Bias within datasets**

Despite the relatively low frequency of jellyfish records, a number of consistent patterns emerge from the different datasets examined, which gives some confidence in some aspects of the results. However, some of the patterns — most obviously the interannual patterns generated by the different sources — are not always in agreement, and certainly the frequency of jellyfish collection by the different methods is vastly different. Before discussing these results, it is thus necessary to explore some of the issues associated with the data collected.

Part of the reason for some discrepancies could be attributed to differences in the areas sampled, as the commercial demersal fishery is not allowed to fish at depths <200 m, where jellyfish are most common (Figure 2), although the independent surveys cover the entire shelf. Some of the inconsistencies between the dependent and independent datasets may also be due to under-reporting: jellyfish were not always recorded by scientists on fisheries-independent surveys (L. Lipinski, Department of Agriculture, Forestry and Fisheries, Cape Town; Graca D’Almeida, Ministry of Fisheries and Marine Resources, Namibia, pers. comm.), but this has changed in more recent time. Also, some of the discrepancies can be attributed to the avoidance of jellyfish by the commercial (especially purse-seine) skippers, for reasons of catch contamination and damage to gear. This could explain the lower overall frequency of jellyfish capture in the fishery-dependent datasets (Table 2).

**Distribution**

**Latitude**

Jellyfish are found along the length of the Namibian coast from the Kunene River in the north to the Orange River in the south (Figure 1). These results are in general agreement with the variously incomplete observations of Venter (1988), Fearon et al. (1992), Sparks et al. (2001) and Lynam et al. (2006). Given their planktonic nature, this implies that benthic polyps of both species are likely to be found along the entire Namibian coast where there is suitable hard substrate. Nothing is known about the distribution of the polyps of...
Aequorea forskalea in the region, but this conclusion is in contrast to that of Fearon et al. (1992) for Chrysaora fulgida, who suggested, on the basis of size frequency data, that polyp beds were located in the north. However, our results are in agreement with the unpublished observations of K Grobler (Ministry of Fisheries and Marine Resources, Lüderitz) and H. Skrypzeck (NatMIRC, Swakopmund) that scyphozoan ephyrae can be collected at a number of locations, including harbours at Walvis Bay (central Namibia) and Lüderitz (in the south), as well as in the north (Pagès and Gili 1992).

Interestingly, our results indicate that peak jelly fish abundance occurs over the central region, which is supported by the term plots showing the response, the proportion of occurrence jellyfish, against predictors Year, Month (Seasonality), Latitude and Depth for separate GAMs. Data from research cruises aboard the RV Dr Fridtjof Nansen (1996–2006) for (a) demersal ($r^2 = 49.2\%$, $n = 1539$) and (b) pelagic samples ($r^2 = 48.8\%$, $n = 316$), and from commercial fisheries for the (c) demersal fleet (1997–2006) ($r^2 = 46.9\%$, $n = 10218$) and (d) the pelagic fleet (1992–2007) ($r^2 = 56.1\%$, $n = 110$). The y-axis is a relative scale, with positive $y$-values on the plots indicating a positive effect of the predictor on the response and a negative $y$-value indicating a negative effect. Shaded regions represent standard errors.
characterised by a broad shelf (Shannon 1985) and a double-shelf break (Barange and Boyd 1992). It has been considered a semi-permanent convergence zone (Boyer et al. 2000), and this could lead to the accumulation of jellyfish (see Graham et al. 2001). Phytoplankton (Estrada and Marrasé 1987, Brown et al. 1991) and zooplankton (Shannon and Pillar 1986, Olivar and Barange 1990) biomass is also higher in the south-central area of the shelf, and both decline to the north. Venter (1988) also observed a peak in jellyfish abundance in this region, but his data were not corrected for effort, and therefore reflect the geographic focus of the pelagic fleet and the distribution of the fish, and not necessarily the jellyfish.

We thus conclude that there is evidence from the literature, unpublished work and the current analysis to suggest that there are polyp beds for *Aequorea forskalea* and *Chrysaora fulgida* more-or-less along the entire Namibian coast, with a likely peak in medusa abundance off central Namibia that could be a consequence of a regional convergence zone.

![Figure 3: Diel changes (day) in the vertical distribution of *Chrysaora fulgida* and *Aequorea forskalea* in the water column at an inshore (120 m) and an offshore (180 m) station sampled off Walvis Bay during August 2003. Number of trawl sets as follows: n = 4 (inshore, day), n = 2 (inshore, night), n = 6 (offshore, day), n = 8 (offshore, night). Mean and SE shown. See Lynam et al. (2006) for more details](image-url)
Cross-shelf
Jellyfish appear to attain greatest abundances in water <200 m depth (Figure 2). This is in agreement with results of other studies in the region (Fearon et al. 1992, Buecher et al. 2001, Sparks et al. 2001). This is not surprising as the genera under study are meroplanktic and are common in shallow coastal seas and embayments elsewhere (e.g. Brodeur et al. 2002, Suchman and Brodeur 2005, Il'inskii and Zavolokin 2007), although Aequorea may extend across the shelf and occur in high abundances beyond the shelf break (Suchman and Brodeur 2005, Suchman et al. in press). Although highest phytoplankton biomass is typically found inshore off Namibia (Estrada and Marrasé 1987, Brown et al. 1991), high zooplankton standing stocks can extend across the shelf and into oceanic waters (Olivar and Barange 1990) and this is mirrored in the distribution of the jellyfish. Many zooplankton species in the region have evolved behavioural mechanisms that allow them to maintain populations over the shelf despite advective losses at the surface (Pillar et al. 1989, Verheyen et al. 1991, Barange and Boyd 1992), and there is some evidence to suggest this may also be the case for at least one of the jellyfish species, Aequorea forskalea (Sparks et al. 2005).

There is thus strong evidence that jellyfish are most abundant in water <200 m depth and that they might have behavioural mechanisms to maintain large populations in this area of intense offshore advection. The slight increase in jellyfish found at depths >600 m (Figure 2) is not considered further, because it likely does not reflect the key species here.

Water column
Although jellyfish can be found throughout the water column, most jellyfish off Namibia are caught in near-surface waters (Figure 3). This is in general agreement with the observations made by Pagès and Gili (1992) from northern Namibia and from the echograms of Utne-Palm et al. (2010) from surveys off central Namibia, as well as from data on both genera elsewhere in the world (e.g. Brodeur 1998, Brodeur et al. 2002).

Greatest concentrations of zooplankton off Namibia are also found in the upper layers of the water column (Olivar and Barange 1990), and given that these organisms have an ability to respond behaviourally to high density patches of food (Bailey and Batty 1983), it suggests that jellyfish are distributing themselves in the most appropriate food environment. In areas with strong thermal stratification, which is not always clear off Namibia (Shannon 1985), zooplankton often display pronounced DVM, migrating from below to above the thermocline, but in areas where turbulent mixing and vertical flows are strong (typically inshore), zooplankton can be found throughout the water column. Although we have been unable to find strong and consistent evidence to indicate that either species displays pronounced DVM (see also Pagès and Gili 1992), Sparks et al. (2001) suggested that C. fuligida tended to be seen more frequently at the water surface during dawn and dusk than at other times. Chrysaora quinquecirrha has been shown in laboratory mesocosms to be negatively phototactic (Schuyler and Sullivan 1997) and to accumulate densely at the surface in darkness, although none of the 15 specimens of Chrysaora hysoscella tagged and individually tracked by Hays et al. (2008) off Ireland displayed DVM. Comparative information on DVM by species of Aequorea is scarce, though Colombo et al. (2003) noted that over the Argentine shelf, populations were dispersed by night throughout the water column, but that they moved into deeper water during the day (see also Brierley et al. 2001).

The failure of populations of either jellyfish species to unambiguously display DVM here could be related to the distribution of zooplankton, because Olivar and Barange (1990) noted that mesozooplankton (as a whole) failed to display clear DVM off central Namibia. Such behaviour is thought to have evolved in response to visual predation pressure (Gliwicz 1986, Lampert 1989), although in environments with vertical differences in horizontal flows (such as upwelling systems), it has the added role of enabling population maintenance. Large jellyfish have relatively few predators and those they have at present are generally, and likely always have been, uncommon (e.g. some sea turtles, sunfish). Given that jellyfish have the ability to respond behaviourally to patches of high food density (Bailey and Batty 1983), and if their food, found mostly in the surface waters, does not perform DVM, we might not expect large jellyfish to show pronounced DVM unless there is some added benefit. However, DVM may be displayed by the jellyfish not at a population behaviour but as an individual behaviour (e.g. Pearre 1973, Gibbons 1993, Hays et al. 2011), and under such circumstances it would be very difficult to detect using the conventional tools employed here (Pearre 1979, Kaartvedt et al. 2007).

In conclusion, we suggest that C. fuligida and A. forskalea are usually found throughout the water column but concentrated in near-surface waters where their zooplankton prey are found, but could in some circumstances perform diel vertical migration.

Seasonality
Jellyfish can be found throughout the year and this is in broad agreement with observations by both Venter (1988) and Fearon et al. (1992). This could be a consequence of the weakly seasonal nature of upwelling off (especially central) Namibia (Shannon 1985), and the presence of abundant zooplankton year-round (Shannon and Pillar 1986, Hutchings et al. 1991). Our data, however, also provide evidence for a winter–spring peak, and this concurs with Venter (1988) who noted jellyfish catches were highest in June–August (although he collected few data outside the pelagic fishing season spanning March–September at that time).

Elsewhere, meroplanktic species of jellyfish tend to show strong seasonal peaks in abundance that can be linked to the cues associated with strobilation and ephyra release (Scyphozoa) or with medusa release (Hydrozoa) and with their subsequent growth and development (e.g. Lucas 2001, Nogueira et al. 2010), as well as with the seasonal movement of water masses (Lynam et al. 2010). Typically, the cue for strobilation is low autumn/winter temperatures (Arai 1997, di Camillo et al. 2010) that result in summer and autumn peaks in abundance, although food (Roosen-Runge 1970) and light (Liu et al. 2009) can also be important. In the case of hydrozoans, salinity (Goy 1973) and light (Elmhirst 1925) can all be important as well as temperature (e.g. Widmer
2004). Given that upwelling is not markedly seasonal over much of the region, and indeed is a near permanent feature at Lüderitz (Shannon 1985), it is likely that ephyrae and small medusa are constantly added to the population throughout the year, although the source location is unknown.

Seasonality in the abundance of medusae, however, does not only reflect the addition of ephyrae or medusae to the population, it also indicates declines in the adult component of the population. Unambiguous information on what causes the latter is largely missing (Mills 1993), and it likely varies with environment. In temperate systems it can be a result of senescence following reproduction (Arai 1997) as well as mortality following a change in temperature/salinity to above/below lethal limits (Sexton et al. 2010). Alternatively, the declining pulsation rates associated with a decrease in temperature could mean that individuals sink (Sexton et al. 2010) and are then more prone to starvation, disease, parasitism (Mills 1993) and predation, as well as physical processes of removal (e.g. Albert 2005). What is clear, however, is that under good conditions, large jellyfish can survive for a relatively long period of time. Albert (2005) has indicated that up to 40% of the Aurelia labiata population in Roscoe Bay (Canada) may live to >2 years of age, and C. fulgida can survive for >20 months in the laboratory (MJG unpublished data). This longevity provides a buffer to population fluctuations and complicates unambiguous interpretation of the data, particularly so if Grön dahl (1988) and Brewer and Feingold (1991) are correct, that the mortality of planulae/polyps is more important in influencing the medusa population size than is the mortality of ephyrae/medusa.

Based on the data presented here and previous work, we suggest that C. fulgida and A. forskalea are found throughout the year but there is reasonable evidence for a winter and early spring peak, although the environmental and biotic conditions controlling the birth and mortality of these jellyfish are currently speculative.

Interannual
Perhaps the most parsimonious way to interpret the lack of a clear, consistent interannual signal in jellyfish abundance in the data reviewed here is to suggest that there has been no change. However, given the methodological limitations and biases associated with the fisheries-independent and fisheries-dependent data, such reasoning would entail a high risk of committing a type II error. Further, it would not follow to extrapolate such a conclusion backwards in time and to suggest that there were as many large jellyfish before the collapse of the pelagic fishery as there are now. Indeed, the present data were collected some 20 years after the collapse, and if the present ecosystem off Namibia is in a new state, then consistent year-on-year changes in jellyfish abundance need not be expected.

A large number of plankton samples were collected and examined for pelagic cnidarians off the south-west coast of Africa prior to the mid-1900s, including those from the Dana (Kramp 1959), Discovery I and II, William Scoresby (Kramp 1957), Deutschen Südpolar (Vanhöffen 1908, 1912, Moser 1925), Deutschen Tiefsee (Valdivia; Vanhöffen 1902a, 1902b, 1911) and Meteor (Leloup 1934) expeditions. Whereas numerous small and large pelagic cnidarians were described by taxonomists from all the above-mentioned collections, of the three large jellyfish presently common off Namibia, viz. A. forskalea, C. fulgida and C. (Dactylometra) africana (Vanhöffen 1902a), only the latter was collected at that time (from Great Fish Bay, South Angola). Yet this species is presently the least common of the three. The other two species were only described from the region during the mid–late 20th century: A. forskalea was first officially recorded off Namibia during the Discovery expeditions in the 1950s (Kramp 1957) and C. fulgida (as C. hysoscella) was first formally identified in the region during the 1990s (Pagès et al. 1992). However, C. fulgida was originally described from the southern Benguela (off the Cape of Good Hope) in the early years of the 19th century, but the poor quality of the original description has led to much subsequent confusion (Neethling 2010). And while Stiasny (1934) considered material collected near Saldanha Bay (RSA) rightly to be C. (hysoscella var.) fulgida, specimens he described from Walvis Bay (Stiasny 1939) as C. fulgida were C. africana (Neethling 2010). A number of regional scientists also collected plankton samples right up until the mid 1960s (e.g. Hart and Currie 1960, Stander and De Decker 1969), and yet they too made no reference to abundant populations of the more conspicuous species of jellyfish.

In our opinion, it is almost inconceivable that the above-listed expeditions would have missed A. forskalea and C. fulgida, yet Mills (2001) has suggested that the routine, undocumented exclusion of jellyfish from plankton samples in earlier years has resulted in an erroneous interpretation of data. There is little support for this argument, because Unterüberbacher (1954) was one of the first regional scientists to study zooplankton in a quantitative way, and he clearly noted that ‘salps, fish larvae and eggs, big ctenophores and medusa’ were removed from samples before analysis. He went on, however, and noted that ‘in some samples the salps occurred in such vast quantities…’ but made no further reference to medusae.

Large jellyfish have undoubtedly ‘always’ been found off Namibia, and the three species in question are indigenous (Neethling 2010), but if the jellyfish were construed to be a ‘problem’ (i.e. occurring at such abundances to have a noticeable impact on fishing or recreation as they have now in some years), then they would inevitably have been reported. The fact that it was not reported constitutes in its own right a strong indication that large jellyfish were likely to be uncommon prior to the 1970s. From the mid-1970s onwards, however, high concentrations of large jellyfish became routinely apparent off Namibia (King and O’Toole 1973, Cram and Visser 1973, Venter 1988, Fearon et al. 1992). The suggestion that jellyfish have increased after the collapse of the large sardine fishery is not new, as Venter (1988) had noted that the abundance and distribution of jellyfish had increased ‘...after the dramatic decrease in pelagic fishing in 1972...’ and that, by the latter half of the 1980s they had ‘...become an increasingly irritating nuisance...’ to regional fishers (Venter 1988, p. 56).

Potential implications
As predators in the plankton, jellyfish have the potential to compete with (especially pelagic) fish for food (Purcell and
Arai 2001), and this is exacerbated in situations where they overlap in time/space (Purcell and Sturdevant 2001, Brodeur et al. 2008, Shoji et al. 2009). Ramifications of this potential interaction are unknown, but can perhaps be presumed to be more negative for fish than for jellyfish, which are able to survive on a far broader range in prey diversity and size. Given that jellyfish can consume large numbers of ichthyo-plankton, as both eggs and larvae (e.g. Purcell and Arai 2001, Brodeur et al. 2002), jellyfish also have the potential to negatively impact fish populations through reducing recruitment. Such has been shown in coastal waters of the North-East Atlantic by Möller (1984) and Lynam et al. (2005).

Direct evidence to show either competition between fish and jellyfish, or predation by jellyfish on fish eggs and larvae off Namibia, is presently missing. However, if one assumes that jellyfish off Namibia can and will eat fish eggs and larvae when they encounter them in the region, then the effect of jellyfish on fish will depend on the spatial and temporal overlap between jellyfish and early life stages of fish, and their respective population sizes. We have shown here that jellyfish peak in abundance in upper layers of the water column, at depths <200 m over the central shelf during winter/spring, which is broadly similar to the distribution of the jellyfish off Namibia, is presently missing. However, if one assumes that jellyfish off Namibia can and will eat fish eggs and larvae when they encounter them in the region, then the effect of jellyfish on fish will depend on the spatial and temporal overlap between jellyfish and early life stages of fish, and their respective population sizes. We have shown here that jellyfish peak in abundance in upper layers of the water column, at depths <200 m over the central shelf during winter/spring, which is broadly similar to the distribution of the spawning products of many of the region’s commercial fish, as summarised in Table 3 and detailed below.

When the sardine biomass was much higher than it is today, they spawned throughout much of the year, albeit with two seasonal maxima: August–October (late winter–spring) and January/February (late summer–autumn) (O’Toole 1977). There were two principal spawning areas, one between 19° and 21° S and one off central Namibia between 22° and 25° S (O’Toole 1977). More recently, Kreiner et al. (2011) found during ichthyoplankton surveys between 1999 and 2005 that the preferred latitude for sardine spawning is around 22°30’S, the area just north of Walvis Bay. Sardine spawn just below the upper mixed layer and eggs ascend rapidly to the surface owing to their buoyancy (Stenevik et al. 2001). Whereas there is a tendency for eggs and larvae to be displaced offshore, larvae can be retained inshore by a combination of behavior and vertical mixing (Stenevik et al. 2001). Anchovy did not dominate the fisheries in Namibia, except in the 1970s when they were subject to heavy fishing pressure, as it was perceived to be a competitor with the more valuable sardine resource (Butterworth 1983). The distribution and movement of anchovy off Namibia used to be similar to that of sardine, but spawning was only significant north of Walvis Bay (Shannon and Pillar 1986), with dense concentrations of larvae found beyond 100 km from the coast (O’Toole 1977, Boyer and Hampton 2001). Deep-water hake M. paradoxus has not been shown to reproduce off Namibia, but shallow-water hake M. capensis do reproduce for much of the year (O’Toole 1978, Olivar et al. 1988), with peak spawning from August to October (Kainge et al. 2007). Spawning occurs

Table 3: Summary of the main observations reported, putative explanations for the observations and their implications for fish

<table>
<thead>
<tr>
<th>Aspect</th>
<th>Variable</th>
<th>Jellyfish observations</th>
<th>Possible reasons</th>
<th>Pertinent fish information and implications</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial</td>
<td>Latitude</td>
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<td>Polyp beds found along entire coastline6–8</td>
<td>Coincident with spawning area for sardine5 and hake2: predation and competition</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Peak in numbers off central Namibia2</td>
<td>Consequence of regional circulation – convergence zone11</td>
<td>Coincident with spawning area for sardine5: predation and competition</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Peak in inshore waters &lt;200 m1,3,4,11</td>
<td>Species meroplanktic and polyp beds likely inshore (ephyrae found very close to coast11, double-cell upwelling2 and possible behavioural mechanisms12</td>
<td>Coincident with distribution of spawning products of small pelagic fish3 and hake2: predation and competition</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Usually found throughout water column but concentrated in near-surface waters1,6,13,14,15</td>
<td>Zooplankton prey concentrated in near-surface waters, and does not generally show strong DVM15</td>
<td>Coincident with distribution of near-surface eggs and larvae of small pelagic fish15 and, eventually, with hake eggs2: predation and competition</td>
</tr>
<tr>
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<td>Seasonal</td>
<td>Found throughout the year1–3, with a late winter–spring peak1,2</td>
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<td>Coincident with spawning peaks of sardine15 and hake2: predation and competition</td>
</tr>
<tr>
<td></td>
<td>Interannual</td>
<td>Conflicting results from pelagic and demersal time-series from research and commercial data over past 15 years1</td>
<td>Biases associated with the fisheries independent and dependent time-series for pelagic and demersal datasets1</td>
<td>Unknown</td>
</tr>
</tbody>
</table>

1 This study; 2 Venter (1988); 3 Fearon et al. (1992); 4 Sparks et al. (2001); 5 Lynam et al. (2006); 6 Pagés and Gili (1992); 7 K Grobler, Ministry of Fisheries and Marine Resources, Lüderitz (pers. comm.); 8 H Skrypzeck, NaMIRC, Swakopmund (pers. comm.); 9 Barange and Boyd (1992); 10 Boyer et al. (2000); 11 Buecher et al. (2001); 12 Sparks et al. (2005); 13 Brierley et al. (2001); 14 Utne-Palm et al. (2010); 15 Olivar and Barange (1990); 16 Kramp (1957, 1959); 17 Vanhöffen (1908, 1912); 18 Moser (1925); 19 Vanhöffen (1902a, 1902b, 1911); 20 Leloup (1934); 21 Kreiner et al. (2011); 22 Kainge et al. (2007); 23 Stenevik et al. (2001); 24 Sundby et al. (2001); 25 O’Toole (1977); 26 Shannon and Pillar (1986); 27 Shannon (1985)
along the length of the Namibian shelf (Olivar and Shelton 1993, Kainge et al. 2007), mostly offshore and at depth (Sundby et al. 2001). Eggs ascend slowly and early larvae are moved onshore and concentrated by a combination of physical and behavioural processes, often in the vicinity of Walvis Bay (Sundby et al. 2001).

In Namibian waters, sardine, anchovy and hake have all shown population declines in the past few decades (although hake catches have been relatively stable since 1990; van der Lingen et al. 2006). This could be, in part, due to the significant overlap between their spawning products and jellyfish. This is additionally supported by the observations of Olivar and Barange (1990) who noted that large jellyfish off Namibia were most common in areas where there were fewer fish larvae. These authors partly attributed this near mutually exclusive distribution to predation of jellyfish on fish larvae. It is noteworthy that this observation was made in April, soon after the second peak in spawning activity of several of these key species, when larvae would be expected to be abundant.

It can be argued that the potential negative impact of jellyfish on fish in the region is supported by the fact that the one commercially important species that has not significantly declined in the region, horse mackerel, appears to have a limited spatial and temporal overlap with jellyfish. Since the collapse of sardine in the late 1960s, horse mackerel catches have gradually increased, and it is presently the largest fishery by volume (Crawford et al. 1987, Boyer and Hampton 2001). The main area of horse mackerel distribution off Namibia is in the north and it extends into southern Angola (Boyer and Hampton 2001), with peak spawning occurring there in summer/autumn (October–March; O’Toole 1977). Taken together, data and arguments presented here suggest that the recovery of pelagic fish populations off Namibia is likely to be hampered in the long term (as tentatively suggested by Boyer et al. 2001), and that the ‘tipping point’ (from a fish-dominated to a jellyfish-dominated system) proposed by Richardson et al. (2009) could have been exceeded, possibly irreversibly (Sommer et al. 2002).

Recommendations for the future

Although the different datasets used here have been useful in improving our understanding of jellyfish abundance seasonally, latitudinally and cross-shelf, there is clearly a marked discrepancy in the interannual abundance estimates (Figure 2). This is a consequence of the fact that none of the surveys from which the datasets arise targeted jellyfish, and indeed often actively avoided them. However, there are a number of improvements that can be made to the collection of jellyfish data in Namibia that would provide more reliable and richer data. At the very least, all catches of jellyfish in fisheries-independent surveys should be routinely recorded, regardless of their size, and preferably additionally in all commercial operations. Ideally this should be done by species (C. fulgida, C. africana and A. forskalea), or at the very least by morpho-species (‘reds’ as Chrysaora spp. and ‘mags’ as Aequorea spp., as termed locally), as this will allow changes in abundance, distribution and seasonality among taxa to be properly assessed. Currently, pelagic landings of jellyfish are not geo-referenced for each set; collection of this information would allow a more detailed description of the habitat preferences, particularly for the different species.

We have provided circumstantial and qualitative evidence that jellyfish could have increased following the sardine collapse in the 1960s, but more extensive evidence, particular quantitative, is lacking and might remain so. Unfortunately, additional data on jellyfish numbers prior to the 1970s will be difficult to find. There appear to be no reliable fisheries records that include jellyfish prior to the 1970s and archived zooplankton samples are lacking, or were conducted after the hypothesised increase (e.g. the South West Africa Pelagic Eggs and Larvae Survey programme in the 1970s). However, it will be easier to establish the size of the current biomass of jellyfish in the system. Our best estimate of jellyfish biomass using acoustic algorithms adapted for jellyfish from August 2003 showed that jellyfish biomass at that time was four times the fish biomass. How representative this estimate is of the typical contemporary jellyfish biomass is not known, but we found here that the commercial and research data for jellyfish around August 2003 did not indicate an unusually high peak of jellyfish biomass (data not shown). This suggests that the large estimated biomass of jellyfish from this survey may be typical. A repeat of the 2003 survey focused on estimating jellyfish and fish biomass using robust acoustic-adapted algorithms developed for jellyfish and fish would provide context for the representativity of the high biomass found then.

There remain many gaps in our knowledge of the biology and ecology of jellyfish species in Namibia that need to be filled. To determine whether jellyfish really are important predators of fish eggs and larvae, dietary studies are needed of both major large jellyfish species, using a combination of direct stomach content analyses (e.g. Flynn and Gibbons 2006) and indirect (stable isotope and fatty acid analyses (e.g. van der Bank et al. 2011) methods. Culturing populations of both main species will enable experiments to determine factors associated with medusa release, growth and senescence, and these should be linked to intensive field surveys of inshore plankton assemblages. Only when work starts across a number of areas will we be in a position to better define and understand the problem and be able to develop management strategies for the future.

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