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

BA Flynn[1], AJ Richardson[2,3], AS Brierley[4], DC Boyer[5,6], BE Axelsen[7], L Scott[8], NE Moroff[5], PI Kainge[5], BM Tjizoo[5] and MJ Gibbons[1]*

[1] *Department of Biodiversity and Conservation Biology, University of the Western Cape, Private Bag X17, Bellville 7535, South Africa*

[2] *Climate Adaptation Flagship, CSIRO Marine and Atmospheric Research, Ecosciences Precinct, GPO Box 2583, Brisbane, Queensland 4001, Australia*

[3] *Centre for Applications in Natural Resource Mathematics (CARM), School of Mathematics and Physics, The University of Queensland, St Lucia, Queensland 4072, Australia*

[4] *Pelagic Ecology Research Group, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife KY16 8LB, UK*

[5] *National Marine Information and Research Centre (NatMIRC), Ministry of Fisheries and Marine Resources, PO Box 912, Swakopmund, Namibia*

[6] *Current address: Orchard Farm, Cockhill, Castle Cary, Somerset BA7 7NY, UK*

[7] *Institute of Marine Research, PO Box 1870 Nordnes, NO-5817 Bergen, Norway*

[8] *UNDP GEF Agulhas and Somali Currents Large Marine Ecosystem (ASCLME) Project, ASCLME House, Private Bag 1015, Grahamstown 6140, South Africa*

* Corresponding author, e-mail: mgibbons@uwc.ac.za

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temporal patterns in distribution of jellyfish off Namibia at a number of scales, using both published and previously unpublished data.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,

pers. comm.) and aquaculture (Doyle et al. 2008) yields, interruptions to coastal power production (jellyfish block cooling intakes), and reduced tourism (jellyfish deter bathers, reviewed in Purcell et al. 2007).

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 finfish 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 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 aurita* 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 Lüderitz (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
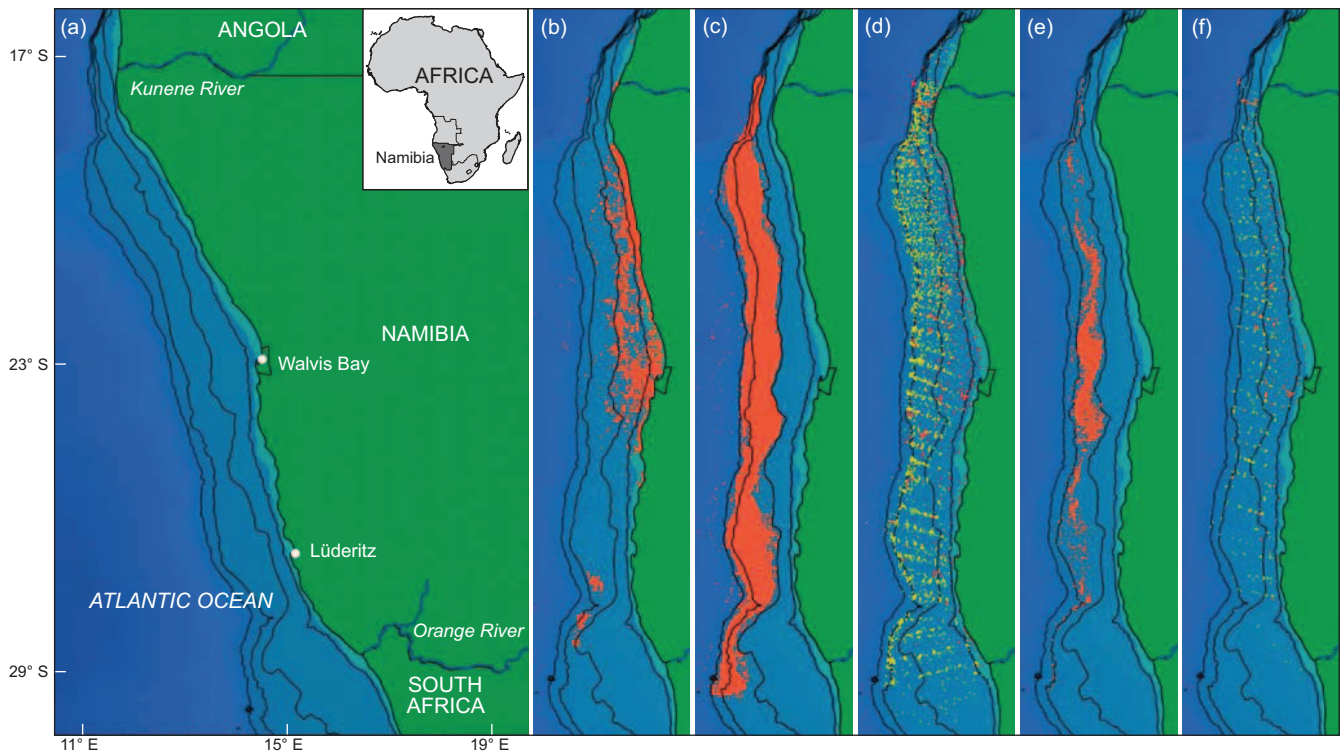
Figure 1: (a) Map of study region showing the geographic location of places mentioned in the text, and bathymetry, (b) seine-net catch positions of the commercial pelagic fleet over the period 1997–2006, (c) demersal trawl positions of the commercial fishery over the period 1997–2006, (d) positions of both demersal (yellow) and pelagic (red) samples collected by the RV *Dr Fridtjof Nansen* over the period 1990–2006, (e) position of positive catches of jellyfish from the commercial demersal fishery over the period 1997–2006, and (f) the positions of demersal (yellow) and pelagic (red) catches of jellyfish by the RV *Dr Fridtjof Nansen* over the period 1990–2006

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 lowering 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

Table 1: Summary of the strengths and weaknesses of the four primary datasets used in this study: (n = number of trawls analysed; frequency = % of trawls/sets containing jellyfish)

Data type	Habitat	n	Frequency (%)	Strengths	Weaknesses
Fisheries-independent (research)	Demersal	3 749	25.03	Spatial: Sampling pelagic habitat randomly; shelf-wide; more sampling in south Other: Data collected by scientific personnel	Spatial: Sampling pelagic habitat for short period Temporal: Not sampled in November/December Other: Jellyfish not reliably counted in early years
	Pelagic	1 147	38.18	Spatial: Sampling the jellyfish habitat directly; more samples from north Other: Data collected by scientific personnel and jellyfish always counted	Spatial: Avoid trawling areas of high jellyfish abundance Temporal: Not sampled in November/December Other: Relatively few trawls
Fisheries-dependent (commercial)	Demersal	363 039	1.66	Spatial: Large number of samples; no latitudinal bias; sampling the pelagic habitat randomly Temporal: Limited bias	Spatial: Sampling pelagic habitat for short period; depth restricted to >200 m, where jellyfish are less common Jellyfish often not recorded Other: Low occurrence
	Pelagic	11 213	20.37	Spatial: Sampling the jellyfish habitat directly Temporal: Limited bias (unfilled quota)	Spatial: Avoid trawling areas of high jellyfish abundance Jellyfish often not recorded or released

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, Valdemarsen 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

large jellyfish off Namibia come from two sources: fishery-dependent data that were obtained from the commercial trawl and purse-seine fisheries and fishery-independent data obtained from regional research surveys and cruises. The former datasets are extensive but have a level of bias, whereas the latter have less bias but are less extensive. The biases of the different datasets are summarised in Table 1, and detailed below.

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_{10}-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

Year	Demersal								Pelagic							
	Dependent				Independent				Dependent				Independent			
	Mean	SD	N_{mo}	N_{samp}	Mean	SD	N_{mo}	N_{samp}	Mean	SD	N_{mo}	N_{samp}	Mean	SD	N_{mo}	N_{samp}
1990	–	–	–	–	0	–	3	198	–	–	–	–	0	–	3	66
1991	–	–	–	–	0	–	6	401	–	–	–	–	0	–	4	153
1992	–	–	–	–	0	–	6	378	19.60	20.12	5	440	0	–	6	127
1993	–	–	–	–	0	–	6	409	–	–	–	–	0	–	5	116
1994	–	–	–	–	0	–	8	619	–	–	–	–	0	–	4	138
1995	–	–	–	–	0	–	7	355	2.46	3.61	5	717	0	–	4	70
1996	–	–	–	–	18.95	25.13	7	534	4.42	6.88	6	569	41.42	47.83	4	137
1997	2.40	2.41	12	8 347	15.40	21.53	6	347	13.90	13.92	10	1 090	17.25	26.47	6	90
1998	3.90	1.89	12	24 573	25.50	33.53	8	514	34.75	12.51	12	1 646	44.43	42.65	8	118
1999	3.73	2.10	12	35 414	23.68	34.96	7	528	35.01	11.56	6	993	58.89	32.41	7	274
2000	2.64	0.85	12	39 436	13.28	8.18	5	291	4.30	6.40	5	214	10.00	17.32	3	15
2001	0.96	0.57	12	43 957	35.66	39.65	5	272	21.87	17.94	8	575	34.98	30.30	3	148
2002	0.69	0.62	12	47 120	21.42	19.48	3	327	25.45	26.00	8	947	–	–	–	–
2003	0.31	0.50	12	45 268	44.77	41.90	4	198	15.03	16.10	9	911	78.35	9.78	2	109
2004	1.32	0.75	12	41 764	41.54	27.06	4	254	28.06	29.93	9	929	32.96	48.69	3	70
2005	0.47	0.68	12	42 142	22.30	20.21	3	254	19.16	18.71	9	803	7.89	–	1	38
2006	0.17	0.37	12	35 018	21.40	25.32	4	230	31.83	35.25	6	590	30.68	49.96	3	148
2007	–	–	–	–	–	–	–	–	15.41	16.76	12	789	–	–	–	–
Grand total	1.66	1.83	120	363 039	25.03	28.18	56	3 749	20.35	20.37	110	11 213	38.18	37.37	40	1 147

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 1998 (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 (M Lipiński, 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
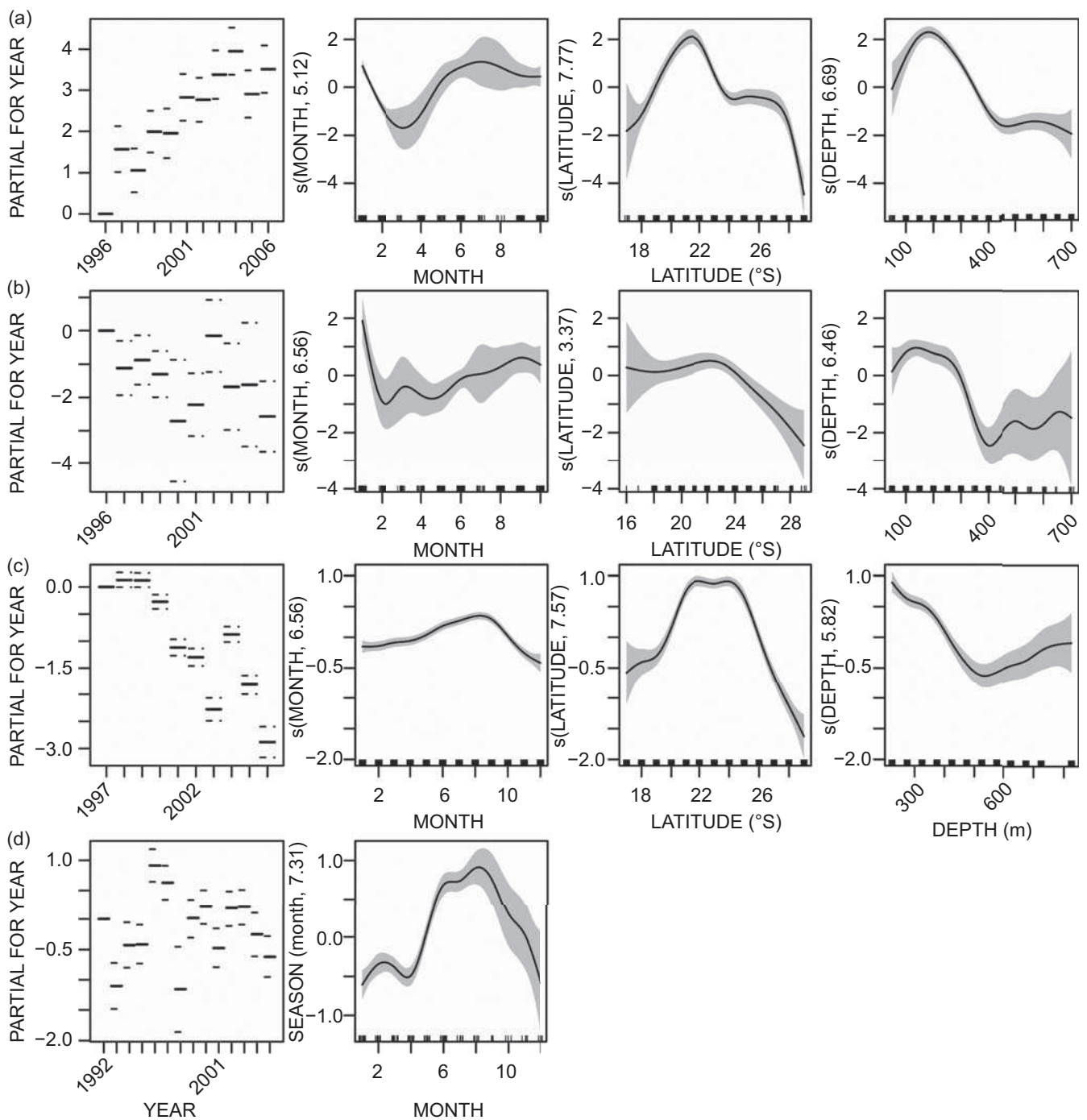
Figure 2: Term plots showing the response, the proportion of occurrence jellyfish, against predictors Year, Month (Seasonality), Latitude and Depth for separate GAMs. Data from research cruises aboard the RV *Dr Fridtjof Nansen* (1996–2006) for (a) demersal (r^2 = 49.2%, n = 1 539) and (b) pelagic samples (r^2 = 48.8%, n = 316), and from commercial fisheries for the (c) demersal fleet (1997–2006) (r^2 = 46.9%, n = 10 218) 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

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 jellyfish abundance occurs over the central region, which is
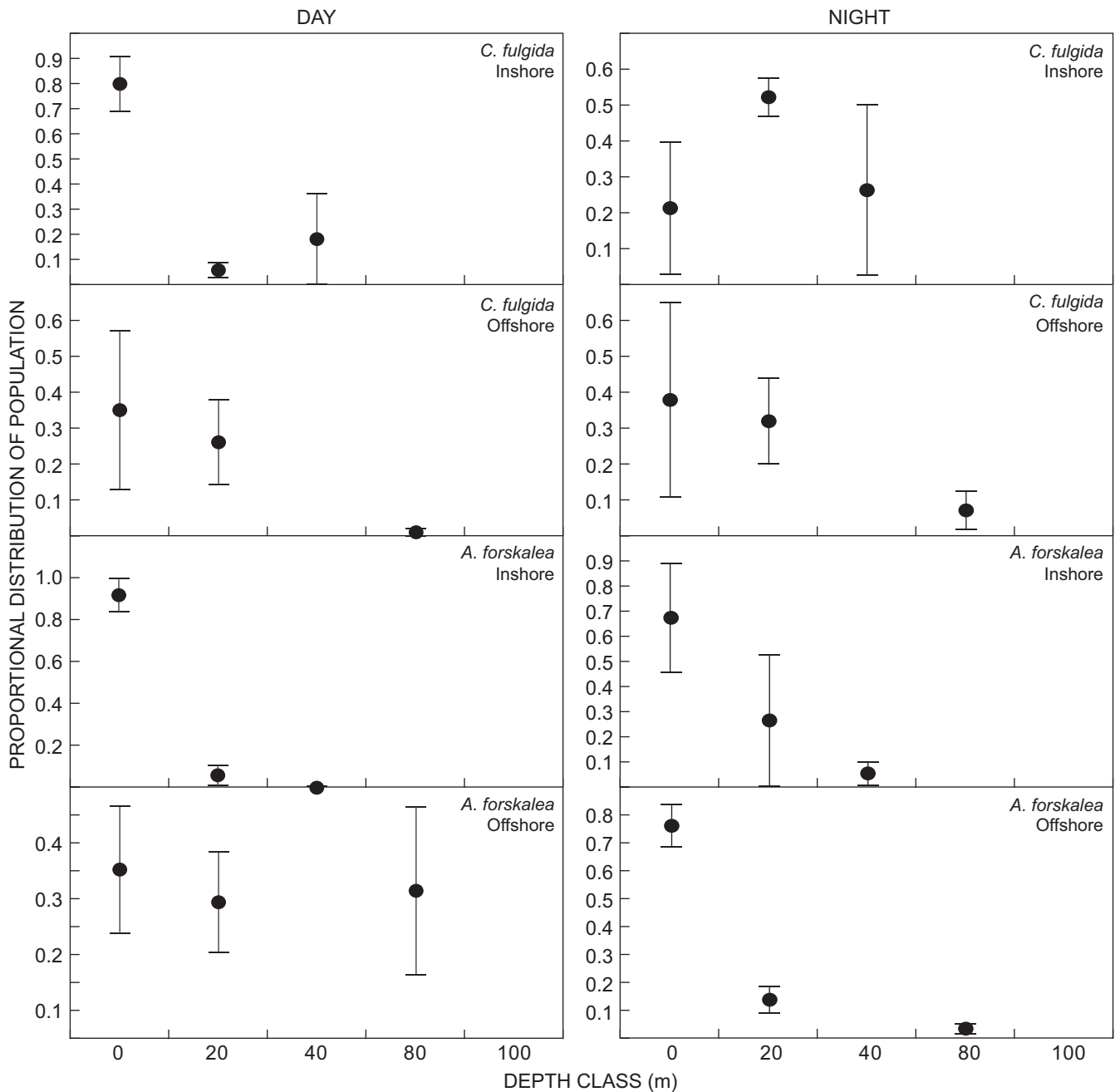
Figure 3: Diel changes (day) in the vertical distribution of *Chrysaora fulgida* and *Aequorea forskalea* in the water column at an inshore (120 m) and an offshore (180 m) station sampled off Walvis Bay during August 2003. Number of trawl sets as follows: *n* = 4 (inshore, day), *n* = 2 (inshore, night), *n* = 6 (offshore, day), *n* = 8 (offshore, night). Mean and SE shown. See Lynam et al. (2006) for more details

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.

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, Verheye 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. fulgida* 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. fulgida* 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 (Elmhirts 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* popula- tion 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 Gröndahl (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) expedi- tions. 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 distribu- tion 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 ichthyoplankton, 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 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

Aspect	Variable	Jellyfish observations	Possible reasons	Pertinent fish information and implications
Spatial	Latitude	Found along entire Namibian coast[1–5]	Polyp beds found along entire coastline[6–8]	Coincident with spawning area for sardine[21] and hake[22]: predation and competition
		Peak in numbers off central Namibia[1,2]	Consequence of regional circulation – convergence zone[9,10]	Coincident with spawning area for sardine[21]: predation and competition
	Cross-shelf	Peak in inshore waters <200 m[1,3,4,11]	Species meroplanktic and polyp beds likely inshore (ephyrae found very close to coast[7,8]), double-cell upwelling[9] and possible behavioural mechanisms[12]	Coincident with distribution of spawning products of small pelagic fish[23] and hake[24]: predation and competition
	Water column	Usually found throughout water column but concentrated in near-surface waters[1,6,13,14]. In some circumstances may perform DVM[4,13]	Zooplankton prey concentrated in near-surface waters, and does not generally show strong DVM[15]	Coincident with distribution of near-surface eggs and larvae of small pelagic fish[25] and, eventually, with hake eggs[24]: predation and competition
Temporal	Seasonal	Found throughout the year[1–3], with a late winter–spring peak[1,2]	Abundant zooplankton prey year-round[26] with a winter peak in upwelling[27]	Coincident with spawning peaks of sardine[25] and hake[22]: predation and competition
	Interannual	Conflicting results from pelagic and demersal time-series from research and commercial data over past 15 years[1]	Biases associated with the fisheries independent and dependent time-series for pelagic and demersal datasets[1]	Unknown

[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, NatMIRC, 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 signifi-cantly 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 collec-tion 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 addition-ally 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 biomasses 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 popula-tions 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.

References

Albert DJ. 2005. Reproduction and longevity of *Aurelia aurita* in Roscoe Bay, a small bay on the Pacific coast of Canada. *Journal of the Marine Biological Association* 85: 575–581.

Arai MN. 1997. *A functional biology of Scyphozoa*. London: Chapman and Hall.

Bailey KM, Batty RS. 1983. Laboratory study of predation by *Aurelia aurita* on larval herring (*Clupea harengus*): experimental observations compared with model predictions. *Marine Biology* 72: 295–301.

Bakun A, Weeks SJ. 2006. Adverse feedback sequences in exploited marine systems: are deliberate interruptive actions warranted? *Fish and Fisheries* 7: 316–333.

Bakun A, Weeks SJ. 2008. The marine ecosystem off Peru: what are the secrets of its fishery productivity and what might its future hold? *Progress in Oceanography* 79: 290–299.

Barange M, Boyd AJ. 1992. Life history, circulation and maintenance of *Nyctiphanes capensis* (Euphausiacea) in the northern Benguela upwelling system. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds), *Benguela trophic functioning. South African Journal of Marine Science* 12: 95–106.

Bartholomae CH, van der Plas AK. 2007. Towards the development of environmental indices of the Namibian shelf, with particular reference to fisheries management. *African Journal of Marine Science* 29: 25–35.

Boyd AJ, Salat J, Masó M. 1987. The seasonal intrusion of relatively saline water on the shelf off northern and central Namibia. In: Payne AIL, Gulland JA, Brink KH (eds), *The Benguela and comparable ecosystems. South African Journal of Marine Science* 5: 107–120.

Boyer DC, Boyer HJ, Fossen I, Kreiner A. 2001. Changes in abundance of the northern Benguela sardine stock during the decade 1990–2000, with comments on the relative importance of fish and the environment. In: Payne AIL, Pillar SC, Crawford RJM (eds), *A decade of Namibian fisheries science. South African Journal of Marine Science* 23: 67–84.

Boyer DC, Hampton I. 2001. An overview of the living marine resources of Namibia. In: Payne AIL, Pillar SC, Crawford RJM (eds), *A decade of Namibian fisheries science. South African Journal of Marine Science* 23: 5–35.

Boyer DC, Cole J, Bartholomae C. 2000. Southwestern Africa: northern Benguela Current region. *Marine Pollution Bulletin* 41: 123–140.

Brewer RH, Feingold JS. 1991. The effect of temperature on the benthic stages of *Cyanea* (Cnidaria: Scyphozoa), and their seasonal distribution in the Niantic River estuary, Connecticut. *Journal of Experimental Marine Biology and Ecology* 152: 49–60.

Brierley AS, Axelsen BE, Boyer DC, Lynam CP, Didcock CA, Boyer HJ, Sparks CAJ, Purcell JE, Gibbons MJ. 2004. Single-target echo detections of jellyfish. *ICES Journal of Marine Science* 61: 383–393.

Brierley AS, Axelsen BE, Buecher E, Sparks C, Boyer H, Gibbons MJ. 2001. Acoustic observations of jellyfish in the Namibian Benguela. *Marine Ecology Progress Series* 210: 55–66.

Brierley AS, Boyer DC, Axelsen BE, Lynam CP, Sparks CAJ, Boyer H, Gibbons MJ. 2005. Towards the acoustic estimation of jellyfish abundance. *Marine Ecology Progress Series* 295: 105–111.

Brodeur RD. 1998. In *situ* observations of the association between juvenile fishes and scyphomedusae in the Bering Sea. *Marine Ecology Progress Series* 163: 11–20.

Brodeur RD, Suchman CL, Reese DC, Miller TW, Daly EA. 2008. Spatial overlap and trophic interactions between pelagic fish and large jellyfish in the northern California Current. *Marine Biology* 154: 649–659.

Brodeur RD, Sugisaki H, Hunt GL. 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* 233: 89–103.

Brotz L, Cheung WWL, Kleisner K, Pakhomov E, Pauly D. In press. Increasing jellyfish populations: trends in large marine ecosystems. *Hydrobiologia.*

Brown PC, Painting SJ, Cochrane KL. 1991. Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. *South African Journal of Marine Science* 11: 537–564.

Buecher E, Sparks C, Brierley A, Boyer H, Gibbons MJ. 2001. Biometry and size distribution of *Chrysaora hysoscella* (Cnidaria, Scyphozoa) and *Aequorea aequorea* (Cnidaria, Hydrozoa) off Namibia, with some notes on their parasite *Hyperia medusarum*. *Journal of Plankton Research* 23: 1073–1080.

Butterworth DS. 1983. Assessment and management of pelagic stocks in the southern Benguela region. In: Sharp GD, Csirke J (eds), *Proceedings of the expert consultation to examine changes in abundance and species composition of neritic fish resources, San José, Costa Rica, April 1983*. San José, Costa Rica: Food and Agriculture Organization. pp 329–405.

Chavez FP, Ryan JP, Lluch-Cota SE, Niquen M. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299: 217–221.

Colombo GA, Mianzan H, Madirolas A. 2003. Acoustic characterization of gelatinous-plankton aggregations: four case studies from the Argentine continental shelf. *ICES Journal of Marine Science* 60: 650–657.

Cram DL, Visser GA. 1973. SWA pilchard stock shows first signs of recovery (summary of results of Phase III of the Cape Cross programme). *South African Shipping News and Fishing Industry Review* 28: 56–63.

Crawford RJM, Shannon LV, Pollock DE. 1987. The Benguela ecosystem. Part IV. The major fish and invertebrate resources. *Oceanography and Marine Biology: an Annual Review* 25: 353–505.

Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon LJ, Verheye HM. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in ''wasp-waist'' ecosystems. *ICES Journal of Marine Science* 57: 603–618.

Cury P, Shannon L. 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography* 60: 223–243.

di Camillo CG, Betti F, Bo M, Martinelli M, Puce S, Bavestrello G. 2010. Constribution to the understanding of the seasonal cycle of *Aurelia aurita* (Cnidaria: Scyphozoa) scyphopolyps in the northern Adriatic Sea. *Journal of the Marine Biological Association of the United Kingdom* 90: 1105–1110.

Doyle TK, de Haas H, Cotton D, Dorschel B, Cummins V, Houghton JDR, Hays GC. 2008. Widespread occurrence of the jellyfish *Pelagia noctiluca* in Irish coastal and shelf waters. *Journal of Plankton Research* 30: 963–968.

Elmhirts R. 1925. Lunar periodicity in *Obelia*. *Nature* 116: 358–359.

Engås A, Skeide R, West CW. 1997. The 'Multisampler': a system for remotely opening and closing multiple codends on a sampling trawl. *Fisheries Research* 29: 295–298.

Estrada M, Marrasé C. 1987. Phytoplankton biomass and productivity off the Namibian coast. In: Payne AIL, Gulland JA, Brink KH (eds), *The Benguela and comparable ecosystems. South African Journal of Marine Science* 5: 347–356.

Fearon JJ, Boyd AJ, Schülein FH. 1992. Views on the biomass and distribution of *Chrysaora hysoscella* (Linné, 1766) and *Aequorea aequorea* (Forskål, 1775) off Namibia, 1982–1989. *Scientia Marina* 56: 75–85.

Feigenbaum DL, Kelly M. 1984. Changes in the lower Chesapeake Bay food chain in the presence of the sea nettle *Chrysaora quinquecirrha* (Scyphomedusae). *Marine Ecology Progress Series* 19: 39–47.

Flynn BA, Gibbons MJ. 2007. A note on the diet and feeding of

Chrysaora hysoscella in Walvis Bay Lagoon, Namibia, during September 2003. *African Journal of Marine Science* 29: 303–307.

Gammelsrød T, Bartholomae CH, Boyer DC, Fillipe VLL, O'Toole MJ. 1998. Intrusion of warm surface water along the Angolan-Namibian coast in February–March 1995: the 1995 Benguela Niño. In: Pillar SC, Moloney CL, Payne AIL, Shillington FA (eds), *Benguela dynamics: impacts of variability on shelf-sea environments and their living resources. South African Journal of Marine Science* 19: 41–56.

Gibbons MJ. 1993. Vertical migration and feeding of *Euphausia lucens* at two 72 h stations in the southern Benguela upwelling region. *Marine Biology* 116: 257–268.

Gliwicz MZ. 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* 320: 746–748.

Goy J. 1973. *Gonionemus suavensis*: structural characters, developmental stages and ecology. *Publications of the Seto Marine Biological Laboratory* 20: 525–536.

Graham WM, Bayha KM. 2007. Biological invasions by marine jellyfish. In: Nentwig W (ed.), *Ecological studies*. Berlin: Springer-Verlag. pp 239–256.

Graham WM, Pagès F, Hamner WM. 2001. A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia* 451: 199–212.

Gröndahl F. 1988. Interactions between polyps of *Aurelia aurita* and planktonic larvae of scyphozoans: an experimental study. *Marine Ecology Progress Series* 45: 87–93.

Hart TJ, Currie RI. 1960. The Benguela Current. *Discovery Reports* 31: 123–298.

Hastie T, Tibshirani R. 1990. *Generalized additive models*. London: Chapman and Hall.

Hays GC, Bastian T, Doyle TK, Fossette S, Gleiss AC, Gravenor MB, Hobson VJ, Humphries NE, Lilley MKS, Pade NG, Sims DW. 2011. High activity and Lévy searches: jellyfish can search the water column like fish. *Proceedings of the Royal Society B* [London] 279: 465–473.

Hays GC, Doyle TK, Houghton JDR, Lilley MKS, Metcalf JD, Righton D. 2008. Diving behaviour of jellyfish equipped with electronic tags. *Journal of Plankton Research* 30: 325–331.

Heymans JJ, Shannon LJ, Jarre A. 2004. Changes in the northern Benguela ecosystem over three decades: 1970's, 1980's and 1990's. *Ecological Modeling* 172: 175–195.

Hutchings L, Pillar SC, Verheye HM. 1991. Estimates of standing stock, production and consumption of meso- and macrozooplankton in the Benguela ecosystem. *South African Journal of Marine Science* 11: 499–512.

Il'inskii EN, Zavolokin AV. 2007. The qualitative composition and autumn-winter distribution of scyphomedusae (Scyphozoa) in the Sea of Okhotsk epipelagial. *Zoologicheskii Zhurnal* 86: 1168–1176 (translated from Russian).

Kaartvedt S, Klevjer TA, Torgersen T, Sørnes TA, Røstad A. 2007. Diel vertical migration of individual jellyfish (*Periphylla periphylla*). *Limnology and Oceanography* 52: 975–983.

Kainge P, Kjesbu OS, Thorsen A, Salvanes AG. 2007. *Merluccius capensis* spawn in Namibian waters, but do *M. paradoxus*? *African Journal of Marine Science* 29: 379–392.

King DPF, O'Toole MJ. 1973. A preliminary report on the findings of the South West African pelagic egg and larval surveys. SFRI Internal Report, Cape Cross Progress Phase III. Sea Fisheries Research Institute, Cape Town.

Kramp PL. 1957. Hydromedusae of the *Discovery* Collections. *Discovery Report* 29: 1–128.

Kramp PL. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. *Dana Report* 46: 1–283.

Kreiner A, Yemane D, Stenevik EK, Moroff NE. 2011. The selection of spawning location of sardine (*Sardinops sagax*) in the northern Benguela after changes in stock structure and environmental conditions. *Fisheries Oceanography* 20: 560–569.

Lampert W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology* 3: 21–27.

Le Clus F, Melo YC, Cooper RM, Malan PE. 1987. The multispecies pelagic fishery off Namibia 1982–1986 and stock assessments for pilchard and anchovy. *Collection of Scientific Papers of the International Commission for Southeast Atlantic Fisheries* 14: 7–25.

Leloup E. 1934. Siphonophores Calycophorides de l'Océan Atlantique tropical et austral. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 10: 1–87.

Liu WC, Lo WT, Purcell JE, Chang HH. 2009. Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. *Hydrobiologia* 616: 247–258.

Lucas CH. 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. *Hydrobiologia* 451: 229–246.

Lynam CP, Attrill MJ, Skogen MD. 2010. Climatic and oceanic influences on the abundance of gelatinous zooplankton in the North Sea. *Journal of the Marine Biological Association of the United Kingdom* 90: 1153–1159.

Lynam CP, Gibbons MJ, Axelsen BA, Sparks CAJ, Coetzee J, Heywood BG, Brierley AS. 2006. Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology* 16: 492–493.

Lynam CP, Heath MR, Hay SJ, Brierley AS. 2005. Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series* 298: 157–167.

Mills CE. 1993. Natural mortality in NE Pacific coastal Hydromedusae: grazing predation, wound healing and senescence. *Bulletin of Marine Science* 53: 194–203.

Mills CE. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451: 55–68.

Mohrholz V, Schmidt M, Lutjeharms JRE, John HC. 2004. Space-time behavior of Angola–Benguela Frontal Zone during the Benguela Niño of April 1999. *International Journal of Remote Sensing* 25: 1337–1340.

Möller H. 1984. Reduction of a larval herring population by jellyfish predator. *Sciences*: 224: 621–622.

Moser F. 1925. Die Siphonophoren der Deutschen Südpolar Expedition 1901–1903. *Deutschen Südpolar Expedition 1901–1903* 17: 1–541.

Neethling S. 2010. Re-descriptions of some southern African Scyphozoa: out with the old and in with the new. MSc thesis, University of the Western Cape, South Africa.

Nogueira Jnr M, Nagata RM, Haddad MA. 2010. Seasonal variation of macromedusae (Cnidaria) at North Bay, Florianópolis, southern Brazil. *Zoologia* 27: 377–386.

Oguz T, Fach B, Salihoglu B. 2008. Invasion dynamics of the alien ctenophore *Mnemiopsis leidyi* and its impact on anchovy collapse in the Black Sea. *Journal of Plankton Research* 30: 1385–1397.

Olivar MP, Barange M. 1990. Zooplankton of the northern Benguela region in a quiescent upwelling period. *Journal of Plankton Research* 12: 1023–1044.

Olivar MP, Rubiés P, Salat J. 1988. Early life history and spawning of *Merluccius capensis* Castelnau in the northern Benguela Current. *South African Journal of Marine Science* 6: 245–254.

Olivar MP, Shelton PA. 1993. Larval fish assemblages of the Benguela Current. *Bulletin of Marine Science* 53: 450–474.

O'Toole MJ. 1977. Investigations into some important fish larvae in the South East Atlantic in relation to the hydrographical environment. PhD thesis, University of Cape Town, South Africa.

O'Toole MJ. 1978. Aspects of the early life history of the hake *Merluccius capensis* Castelnau off South West Africa. *Fisheries Bulletin South Africa* 10: 20–36.

Pagès F, Gili JM. 1992. Influence of the thermocline on the vertical migration of medusa during a 48 h sampling period. *South African Journal of Zoology* 27: 50–59.

Pagès F, Gili JM, Bouillon J. 1992. Planktonic cnidarians of the Benguela Current. *Scientia Marina* 56: 1–144.

Pearre S. 1973. Vertical migration and feeding in *Sagitta elegans* Verrill. *Ecology* 54: 300–314.

Pearre S. 1979. Problems of detection and interpretation of vertical migration. *Journal of Plankton Research* 1: 29–44.

Pillar SC, Armstrong DA, Hutchings L. 1989. Vertical migration, dispersal and transport of *Euphausia lucens* in the southern Benguela Current. *Marine Ecology Progress Series* 53: 179–190.

Purcell JE, Arai MN. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia* 451: 27–44.

Purcell JE, Sturdevant MV. 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Marine Ecology Progress Series* 210: 67–83.

Purcell JE, Uye SI, Lo WT. 2007. Anthropogenic causes of jellyfish blooms and direct consequences for humans: a review. *Marine Ecology Progress Series* 350: 153–174.

Richardson AJ, Bakun A, Hays GC, Gibbons MJ. 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution* 24: 312–322.

Roosen-Runge EC. 1970. Life cycle of the hydromedusae *Phialidium gregarium* (A. Agassiz, 1862) in the laboratory. *The Biological Bulletin* 139: 203–221.

Rouault M, Illig S, Bartholomae C, Reason CJC, Bentamy A. 2007. Propagation and origin of warm anomalies in the Angola Benguela upwelling system in 2001. *Journal of Marine Systems* 68: 473–488.

Sætersdal G, Bianchi G, Strømme T, Venema SC. 1999. The *Dr Fridtjof Nansen* Programme 1975–1993. Investigations of fishery resources in developing countries. History of the programme and review of results. *FAO Fisheries Technical Paper* 391: 1–434.

Schülein FH, Butterworth DS, Cram DL. 1978. An assessment of the southeast Atlantic pilchard population in ICSEAF divisions 1.4 and 1.5, 1953–1977. *Collection of Scientific Papers of the International Commission for Southeast Atlantic Fisheries* 5: 35–44.

Schuyler Q, Sullivan BK. 1997. Light responses and diel migration of the scyphomedusa *Chrysaora quinquecirrha* in mesocosms. *Journal of Plankton Research* 19: 1417–1428.

Sexton MA, Hood RR, Sarkodee-adoo J, Liss AM. 2010. Response of *Chrysaora quinquecirrha* medusa to low temperature. *Hydrobiologia* 645: 125–133.

Shackleton LY. 1987. A comparative study of fossil fish scales from three upwelling regions. In: Payne AIL, Gulland JA, Brink KH (eds), *The Benguela and comparable ecosystems. South African Journal of Marine Science* 5: 79–84.

Shannon LV. 1985. The Benguela ecosystem. I. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology: an Annual Review* 23:105–182.

Shannon LV, Boyd AJ, Brundrit GB, Taunton-Clarke J. 1986. On the existence of an El Niño-type phenomena in the Benguela system. *Journal of Marine Research* 44: 495–520.

Shannon LV, Pillar SC. 1986. The Benguela Ecosystem. Part III. Plankton. *Oceanography and Marine Biology: an Annual Review* 24: 65–170.

Shoji J, Mizuno K-I, Yamamoto M, Miller TW, Hamaoka H, Omori K. 2009. Spatial distribution and dietary overlap between Japanese anchovy *Engraulis japonicus* and moon jellyfish *Aurelia aurita* in the Seto Inland Sea, Japan. *Scientia Marina* 73S1: 191–198.

Sommer U, Stibor H, Katechakis A, Sommer F, Hansen T. 2002. Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: primary production. *Hydrobiologia* 484: 11–20.

Sparks C, Brierley AS, Buecher E, Boyer D, Axelsen BE, Gibbons MJ. 2005. Submersible observations on the daytime vertical distribution of *Aequorea forskalea* off the west coast of South

Africa. *Journal of the Marine Biological Association of the United Kingdom* 85: 519–522.

Sparks C, Buecher E, Brierley AS, Boyer H, Axelsen BE, Gibbons MJ. 2001. Observations on the distribution and relative abundance of the scyphomedusan *Chrysaora hysoscella* (Linné, 1766) and the hydrozoan *Aequorea aequorea* (Forskål, 1775) in the northern Benguela ecosystem. *Hydrobiologia* 451: 275–286.

Stander GH, De Decker AHB. 1969. Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. *Investigational Report, Division of Sea Fisheries, South Africa* 81: 1–46.

Stenevik EK, Sundby S, Cloete R. 2001. Influence of buoyancy and vertical distribution of sardine *Sardinops sagax* eggs and larvae on their transport in the northern Benguela ecosystem. In: Payne AIL, Pillar SC, Crawford RJM (eds), *A decade of Namibian fisheries science. South African Journal of Marine Science* 23: 85–97.

Stiasny G. 1934. Scyphomedusae. *Discovery Report* 8: 329–396.

Stiasny G. 1939. Über *Dactylometra fulgida* (Reynaud) von der Walfischbai. *Zoologischer Anzeiger* 126: 172–185.

Strømme T, Iilende T. 2001. Precision in systematic trawl surveys as assessed from replicate sampling by parallel trawling off Namibia. In: Payne AIL, Pillar SC, Crawford RJM (eds), *A decade of Namibian fisheries science. South African Journal of Marine Science* 23: 385–396.

Suchman CL, Brodeur RD. 2005. Abundance and distribution of large medusa in surface waters of the northern California Current. *Deep-Sea Research II* 52: 51–72.

Suchman CL, Brodeur RD, Emmert RL, Daly EA. In press. Large medusa in surface waters of the northern California Current: variability in relation to environmental conditions. *Hydrobiologia.*

Sundby S, Boyd AJ, Hutchings L, O'Toole MJ, Thorisson K, Thorsen A. 2001. Interaction between Cape hake spawning and the circulation in the northern Benguela upwelling ecosystem. In: Payne AIL, Pillar SC, Crawford RJM (eds), *A decade of Namibian fisheries science. South African Journal of Marine Science* 23: 317–336.

Thomas RM. 1986. The Namibian pilchard: the 1985 season, assessment for 1952–1985 and recommendations for 1986. *Collection of Scientific Papers of the International Commission for Southeast Atlantic Fisheries* 13: 243–269.

Unterüberbacher HK. 1964. Zooplankton studies in the waters off Walvis Bay with special reference to the Copepoda. *Investigational Reports of the Marine Research laboratory, South West Africa* 11: 1–42.

Utne-Palm AC, Salvanes AGV, Currie B, Kaartvedt S, Nilsson GE, Baithwaite V, Stecyk JAW, Hundt M, Flynn B, van der Bank M, Peard KR, Lunde IG, Sandvik GK, Klevjer TA, Pittman K, Sweetman AK, Strandabø RAU, Gibbons MJ. 2010. Trophic structure and community stability in an overfished ecosystem. *Science* 329: 333–336.

Valdemarsen JW, Misund OA. 1994. Trawl designs and techniques used by Norwegian research vessels to sample fish in the pelagic zone. In: Hylen A (ed.), *Proceedings of the sixth PRIW-PEW0 symposium.* Bergen: Institute of Marine Research. pp 135–144.

van der Bank MG, Utne-Palm AC, Pittman K, Sweetman AK, Richoux NB, Brüchert V, Gibbons MJ. 2011. Dietary success of a 'new' key fish in an overfished ecosystem: evidence from fatty acid and stable isotope signatures. *Marine Ecology Progress Series* 428: 219–233.

van der Lingen CD, Shannon LJ, Cury P, Kreiner A, Moloney CL, Roux J-P, Vaz-Velho F. 2006. Resource and ecosystem variability, including regime shifts, in the Benguela Current system. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney C, Woods J. (eds), *Benguela: predicting a large marine ecosystem.* Amsterdam: Elsevier. pp 147–184.

van der Westhuizen A. 2001. A decade of exploitation and management of the Namibian hake stocks. In: Payne AIL,

Pillar SC, Crawford RJM (eds), *A decade of Namibian fisheries science. South African Journal of Marine Science* 23: 307–315.

Vanhöffen E. 1902a. Die acraspeden medusen der Deutschen Tiefsee-Expedition 1898–1899. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* 3: 1–52.

Vanhöffen E. 1902b. Die craspeden medusen der Deutschen Tiefsee-Expedition 1898–1899. 1. Trachymedusen. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* 3: 55–86.

Vanhöffen E. 1908. Die Lucernariden und Skyphomedusen der Deutschen Südpolar Expedition 1901–1903. *Deutschen Südpolar Expedition 1901–1903* 10: 25–59.

Vanhöffen E. 1911. Die Anthoathecata und Leptothecata der Deutschen Tiefsee Expedition 1898–1899. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* 19: 193–233.

Vanhöffen E. 1912. Die craspedoten Medusen der Deutschen Südpolar Expedition 1901–1903. *Deutschen Südpolar Expedition 1901–1903* 13: 351–396.

Venter GE. 1988. Occurrence of jellyfish on the west coast off South West Africa/Namibia. *Report of the South African National Science Programmes* 157: 56–61.

Verheye HM, Hutchings L, Peterson WT. 1991. Life history and population maintenance strategies of *Calanoides carinatus* (Copepoda: Calanoida) in the southern Benguela ecosystem. *South African Journal of Marine Science* 11: 179–191.

Widmer CL. 2004. The hydroid and early medusa stages of *Mitrocomella cellularia* (Hydrozoa, Mitrocomidae). *Marine Biology* 145: 315–321.

Wood SN. 2006. *Generalized additive models: an introduction*. London: Chapman & Hall/CRC Press.