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A COMPARATIVE REVIEW OF MACROMEDUSAE IN EASTERN BOUNDARY CURRENTS

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Abstract The productive eastern boundary current (EBC) systems provide significant sources of global marine protein and have been subject to intense research over the last 50 years. Yet large jellyfish, which are present in all four major systems, have seldom been included in otherwise comprehensive reviews. This undoubtedly reflects their lack of intrinsic commercial value, and the consequently slow pace of knowledge generation. We attempt to redress that imbalance here and to consolidate disparate information on the macromedusae of EBC systems. With the exception of the Canary Current system, which supports a generally low biomass of mostly subtropical taxa,

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jellyfish assemblages in the Benguela, Humboldt and California Current systems are dominated by cool water taxa that can occur at high abundances. While there are large gaps in knowledge, which are highlighted, it is clear that jellyfish can play significant ecological roles in each system. Although there may be strong similarities in faunal composition among the different systems, there are pronounced differences in population responses to the environment and in system resilience and these are reviewed and discussed.

Keywords: Biogeography; Coastal Upwelling; Cnidaria; Ecology; Ecosystem; Fisheries; Medusozoa.

Introduction

The four main eastern boundary current (EBC) systems are located along the western coastlines of continents bordering both the Pacific (California, Humboldt) and Atlantic (Canary, Benguela) Oceans. They are characterized by very high productivity and short food chains, and are collectively responsible for >20% of global capture fisheries (Ryther 1969, Schwartzlose et al. 1999, Rykaczewski & Checkley 2008), contributing significantly to regional employment and local economies (Ommer et al. 2009). All four systems are characterized by wind-driven coastal upwelling: upwelled water delivering new nitrogen into the euphotic zone over generally narrow continental shelves (Barber & Smith 1981). They are regarded as naturally eutrophic systems, and the abundant nitrate fuels productive phytoplankton communities dominated by large cells (principally diatoms), whose energy and materials in turn feed into largely herbivorous zooplankton (calanoid copepods and euphausiids) and/or omnivorous filter- and particulate-feeding small fishes, principally clupeoids (Chavez & Messié 2009). Any mismatch between cycles of phytoplankton production and consumption results in sedimentation, leading to bottom waters with often hypoxic characteristics (Grantham et al. 2004). It has been suggested that these ecosystems are characterized as having a “wasp-waist” structure in which low species diversity at middle trophic levels can strongly impact the structure of the entire ecosystem by influencing the biomass of both its predators and prey through bottom-up and top-down controls (or “middle-out” trophic controls), respectively (Cury et al. 2000 *cf* Fréon et al. 2009).

Given their pivotal role in food security, upwelling ecosystems have been and continue to be, the subject of extensive research. Whilst much of this is specific to individual EBCs as it pertains to the regional management of local resources, the four systems generally share substantial organisational structure, with greater similarities among the systems that share ocean basins (e.g. the two Pacific and the two Atlantic EBCs). In their analysis of the wasp-waist structure of the four EBC systems, Fréon et al. (2009) subdivided each into four (latitudinally and bathymetrically) arguing that shelf and offshelf areas function slightly differently and that each system has a natural internal boundary separating water with colder and warmer temperate affinities. Despite some simplifying assumptions in their approach, Fréon et al.’s (2009) analyses demonstrate greater similarities between the composition and structure of the Pacific EBCs, relative to the two Atlantic Ocean EBCs (Fréon et al. 2009) (but see Figure 1). While each system has a number of endemic species (genera and families), a surprising number of taxa are shared between systems (Table 1). Sardines (*Sardinops*), anchovies (*Engraulis*), and chub and horse mackerels (*Scomber* and *Trachurus*, respectively) immediately come to mind. However, these common taxa are not confined to coastal pelagic and large migratory species, as they also include many members of the plankton, including jellyfish (Table 1). At the time that Fréon et al. (2009) undertook their analyses, jellyfish were deliberately excluded owing to a lack of information. Yet, as we outline below, jellyfish can be conspicuous components of EBC systems and there are some strong commonalities between them.

Our understanding of jellyfish populations in EBC systems is meagre and, at times, contradictory. Whilst jellyfish populations naturally undergo intra-annual fluctuations in abundance that reflect the interaction of species-specific responses to the environment (Fernández-Alías et al. 2020) and processes of aggregation and accumulation at frontal regions and in embayments

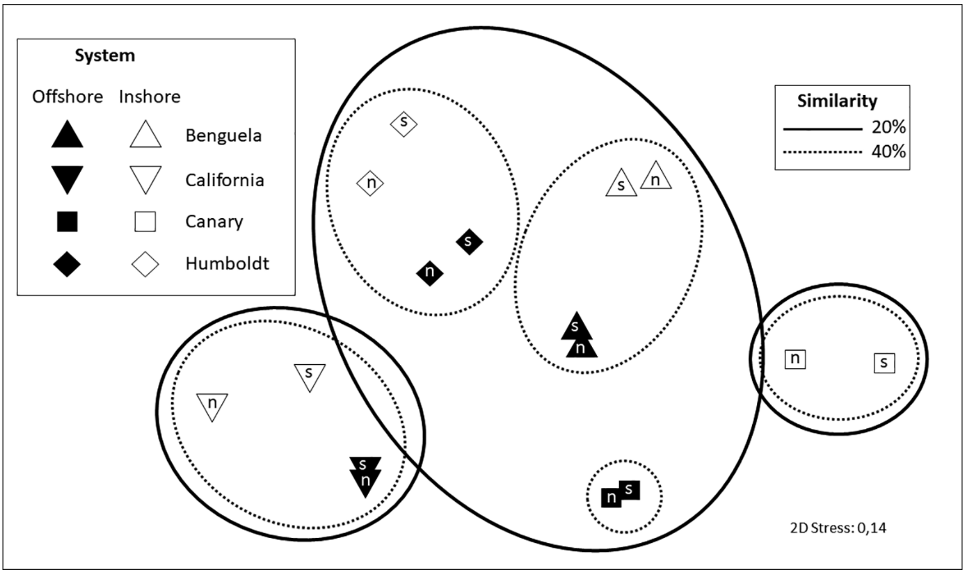

Figure 1 Non-metric multidimensional scaling plot showing the similarity (Bray Curtis Index, presence absence) between the generic composition of sub-systems within the four major EBC systems considered here. Data restricted to smaller functional groups only (plankton, cephalopods and small pelagic fishes); reanalysed from Fréon et al. (2009) using PRIMER software. Key to EBC systems and subsystems (inshore, offshore) provided; n, northern; and southern, s.

Table 1 Number of genera found in one, two, three or all four of the EBC systems considered here, by functional group

Functional group	Unique to one EBC system	Shared between two EBC systems	Shared between three EBC systems	Shared between four EBC systems	Total number of genera
Baleen Whales	2	–	1	1	4
Cephalopods	7	5	–	1	13
Chaetognaths	2	–	–	4	6
Copepods	6	3	3	2	14
Demersal fish	34	2	–	1	37
Diatoms	9	3	3	1	16
Dinoflagellates	6	4	2	1	13
Dolphins and toothed whales	3	7	4	2	16
Euphausiids	–	–	3	2	5
Inshore large pelagic fish	7	4	1		12
Medium-sized pelagic fish	–	1	–	2	3
Mesopelagic fish	13	3	–	–	16
Offshore large pelagic fish	1	–	1	2	4
Pinnipeds	7	–	1	–	8
Seabirds	18	9	2	2	31
Sharks and rays	11	3	5	10	29
Small pelagic fish	7	–	1	1	9
Macromedusae	*Rhizostoma*	*Aurelia*	*Chrysaora, Aequorea*	*Pelagia*	5

Source: Data reanalysed from Fréon et al. (2009).

Note: Genera considered are those that contribute towards 90% of the biomass in each functional group.

(Graham et al. 2001), there is some evidence to suggest that at the global level, jellyfish populations are increasing monotonically in some systems. Without attempting to explain the drivers, Condon et al. (2013) have suggested that jellyfish populations undergo 20-year oscillations in size at the global scale and that we are presently in an upward phase. That said, at a regional-scale their dataset indicates that populations in the California Current have declined since records began, whilst those in the Benguela and the Humboldt systems have neither increased nor decreased (Condon et al. 2013). These results differ from those of Brotz et al.'s (2012) global analysis of jellyfish populations in large marine ecosystems (LMEs) using "soft" data. The latter authors have suggested that there have been recent increases in the Benguela and California Current systems, but a decrease in the Humboldt system. The data used by Brotz et al. (2012) required the assignment of a confidence level to assessed trends, and these were regarded as "high" for the Humboldt and Benguela systems but (perhaps surprisingly) "low" for the California Current system. Nothing substantive is known about changes in the long-term dynamics of jellyfish populations in the Canary Current EBC. Although our understanding of jellyfish has increased in the last few decades (e.g. Gibbons & Richardson 2013), this increase in focused research and knowledge has not been evenly spread across the world's ecosystems, and surprisingly little has actually been conducted in EBC systems, despite their obvious importance.

What are jellyfish?

Jellyfish are organisms whose body tissues comprise >95% water (Lucas & Dawson 2014) and include representatives from three phylogenetically very distinct taxa (Giribet & Edgecombe 2020): Ctenophora, Cnidaria and Chordata (Thaliacea). Salps, pyrosomes and doliolids (Thaliacea) are strictly epipelagic filter feeders, pumping water across mucous nets that are fine enough to trap bacteria and micro-phytoplankton. They play an important role in the biological carbon pump, turning surface production into fast-sinking faecal pellets and marine snow. Salps, pyrosomes and (especially) doliolids have complex life cycles involving an alteration between sexual and asexual generations, with sexual individuals being hermaphroditic. By contrast, ctenophores are strictly carnivorous, either by capturing mesozooplankton prey on colloblast-laden surfaces or by engulfing (usually) other ctenophores whole. They are hermaphroditic and are capable of reproducing at a small size. Whilst a few taxa are benthic, most ctenophores are pelagic and can be found in all layers of the ocean from the surface to the bathyal.

The phylum Cnidaria comprises three subphyla, only one of which includes pelagic, free-living members: Medusozoa (Kayal et al. 2013). As their name suggests, medusozoans typically (and ancestrally) display an alteration of generations (metagenesis) between a (usually) benthic polyp that reproduces asexually and a free-swimming medusa that reproduces sexually (sexes are generally separate). That said, the medusa phase may be lost in some taxa, whilst the sessile polyp phase may be lost in others. All cnidarians are carnivorous, capturing prey on nematocyst-laden surfaces in a variety of ways, although some shallow water taxa also contain photosynthetic zooxanthellae. Like ctenophores, pelagic cnidarians can be found in all oceans and at all depths, although taxa that have retained a metagenic life history are generally more common in shallow water over continental shelves.

Despite their differences, the three distinct taxa share an ecological commonality: they all have members whose populations have the potential to increase very rapidly and can strongly influence energy flow within the ecosystems in which they occur (Lucas & Dawson 2014). Although all three taxa are found in EBC systems, thaliaceans are generally (e.g. Thiriot 1978), but not always (Martin et al. 2017, Miller et al. 2019), uncommon in nearshore waters. Our knowledge of ctenophores in upwelling ecosystems is limited, perhaps because of their fragility and reluctance to fix and preserve well, although more robust species such as *Pleurobrachia* can be found in abundance in enclosed embayments (e.g. Gibbons et al. 2003). Medusozoans, however, can be abundant.

The subphylum Medusozoa comprises three classes with medusoid members: Hydrozoa, Cubozoa and Scyphozoa. The medusa phase, when present, differs widely in size among the different classes, with those of scyphozoans generally being larger than those of cubozoans, which in turn are larger than those of hydrozoans, with some exceptions. Of the three classes, scyphozoans are certainly more conspicuous in EBC systems, although ecological information about the other two is relatively scant.

The possession of a metagenic life cycle confers a distinct advantage to jellyfish that is otherwise denied to species with a holopelagic life style (including forage fish), because polyps allow populations to persist in an area when surface advection may export medusae or when environmental conditions no longer favour the survival of medusae. Polyps and medusae can survive in waters with a low concentration of dissolved oxygen, and when food densities decline to the point of starvation, some medusae (and polyps) may metabolise body tissues and shrink before regrowing again when the ambient food environment improves. Jellyfish do not require light in order to feed on mesozooplankton (unlike particulate-feeding fishes), and their often-large size, when combined with their low carbon content, makes them no less efficient than fish when feeding (Acuña et al. 2011). Indeed, their growth rates resemble those of some clupeoid fish (Palomares & Pauly 2009).

In the preceding paragraph, we have deliberately drawn comparisons between jellyfish (principally scyphozoans) and (small pelagic) fishes because both are effectively members of the same trophic guild. Both have the ability to feed on the young of each other and themselves (Irigoien & De Roos 2011) and both feed at a broadly similar trophic level. Significant research has been conducted on the dynamics of pelagic fish populations in EBC systems for intuitive reasons, such as their tremendous commercial fisheries role and their great importance to many higher trophic-level predators. Population shifts between anchovy and sardine (the dominant two species) have been recorded in most systems (Schwartzlose et al. 1999, Checkley et al. 2009), and there is evidence to suggest that these are likely caused by climate variability, but may also be secondarily affected by competition, predation and fishing (Chavez et al. 2003, Tourre et al. 2007).

Scope of this review

A considerable amount of research has been conducted on the environment and the exploitable living resources of EBC systems, for obvious reasons. Although this work has been reviewed and synthesized extensively (e.g. Benguela – Shannon et al. 2006, Humboldt – Thiel et al. 2007, Canary – Arístegui et al. 2009, California – Checkley & Barth 2009), none of these contributions have incorporated jellyfish in a meaningful way, despite the fact that they can be abundant in all systems at some time. Part of the reason for their exclusion reflects a lack of knowledge, which in turn reflects their commercial value: fisheries laboratories often lack the resources to devote to studying anything that does not contribute directly to the economy. As a consequence, the research that has been conducted on jellyfish has tended to be done by scientists from outside national laboratories, often with external international support, or by interested government biologists when the opportunity arises. The nature of the beast is such that chance plays a big role in jellyfish science, and as such the knowledge acquired has taken time to accumulate to the point that syntheses can be made. However, we believe that the time is ripe for a first review of knowledge of jellyfish in three of the four major EBC systems, and we attempt to do that here.

We have structured our review as follows. For each EBC system, which approximates an LME *sensu* Sherman & Alexander (1986) and not a regional sea (Sheppard 2019), we briefly recapitulate salient features of the biophysical environment in order to contextualize the species observed. The emphasis is on brief, as all systems have been the subject of previous reviews (see above). We then provide an overview of the jellyfish species present, their distribution in space and time, and summarize key biological processes. We look at the ecological role these organisms play within the EBC systems as predators and prey, their interactions with local economies and how they have been included in ecosystem models. We have taken this more functional approach, rather than a species-by-species account, as we believe it is easier to compare across taxa and it allows readers to make their own generalizations. We have deliberately confined our review to information that has been generated within the four EBC systems dealt with here: knowledge about any EBC species that has been created from outside the EBC systems has not been considered. Whilst we acknowledge that this may not satisfy all readers, it should be remembered that a species' ecology is likely context dependent (e.g. Swift & Dawson 2020). It should also be noted that we frequently refer to seasons in the text, and we do this without consistent reference to boreal or austral for comparative purposes. In the Benguela and Humboldt EBC systems, spring is regarded as September–November, summer as December–February, autumn as March–May and winter as June–August.

We conclude the review by attempting to put our observations in a phylogenetic context, by synthesising ecological knowledge across systems and by highlighting gaps and constraints. This has not been an easy task as different questions have been asked of jellyfish in the four EBC systems, and not all have been equally studied. Specifically, data for the Canary Current system are very patchy, and our account in this regard is based largely on qualitative and anecdotal data. However, we have taken the decision to include this scant knowledge for the sake of completeness and to highlight the issues faced by jellyfish scientists in developing countries. We stress at the outset that some of the data used here have yet to see the light of day in the peer-reviewed literature and some of the analyses use published data in a way that differs from the original.

The Benguela ecosystem

Description

The Benguela ecosystem spans the western coastline of southern Africa, from southern Angola and the seasonally shifting Angola:Benguela front in the north (~17°S) to the southernmost extension of the Agulhas Bank at ~37°S (Hutchings et al. 2009). The landmass is orientated approximately N–S for the most part, although along the south coast of South Africa, it has a W–E orientation (Figure 2). The continental shelf is broad over the western part of the Agulhas Bank, in the area of the Orange River cone and off central Namibia (Walvis Bay); it is narrowest at Cape Point, Cape Columbine, Lüderitz and Cape Frio (Figure 2). The seabed is for the most part composed of soft sediments, and rocky substrata are largely restricted to headlands at the aforementioned capes and peninsulas and inshore islands. Offshore, the sediments are largely of biogenic origin, whilst inshore they are predominantly terrigenous (Rogers & Bremner 1991).

Unlike all other EBCs, that of the Benguela is bounded to the north and south by warm subtropical waters: the Angola Current in the north and the Agulhas Current in the south (Figure 2). The position of the Angola:Benguela front is dynamic and shifts seasonally to reflect the relative intensities of upwelling in northern Namibia and the Angola Current (Shannon 1985); interannual changes reflect ENSO events and zonal wind stress in the equatorial Atlantic (Florenchie et al. 2003). Occasionally, large quantities of warm, oxygen-poor water flow into the northern region (Rouault et al. 2007, Rouault 2012). The Agulhas Current, which tracks the edge of the Agulhas Bank and retroflects eastward at ~39°S, may similarly influence the Benguela ecosystem through eddies, rings and filaments that are shed into the South Atlantic (Lutjeharms 2006).

The interaction between the South Atlantic high and the continental low-pressure systems results in onshore winds, which, owing to the orientation of the landmass, its orography and deserts, favour coastal upwelling (Shannon 1985). Upwelling is, for the most part, seasonal, being maximal in spring and early summer and is most intense at the aforementioned capes and peninsulas (Shannon 1985). It is particularly strong and relatively aseasonal at Lüderitz (~26°S) in southern Namibia, and upwelling here effectively divides the system into northern and southern sub-systems (Shannon 1985). Circulation in the northern Benguela is less dynamic than in the south owing to the wider shelf there, and a double-circulation cell is seen off central Namibia (shelf break and continental slope) that effectively traps water over the shelf (Barange et al. 1992).

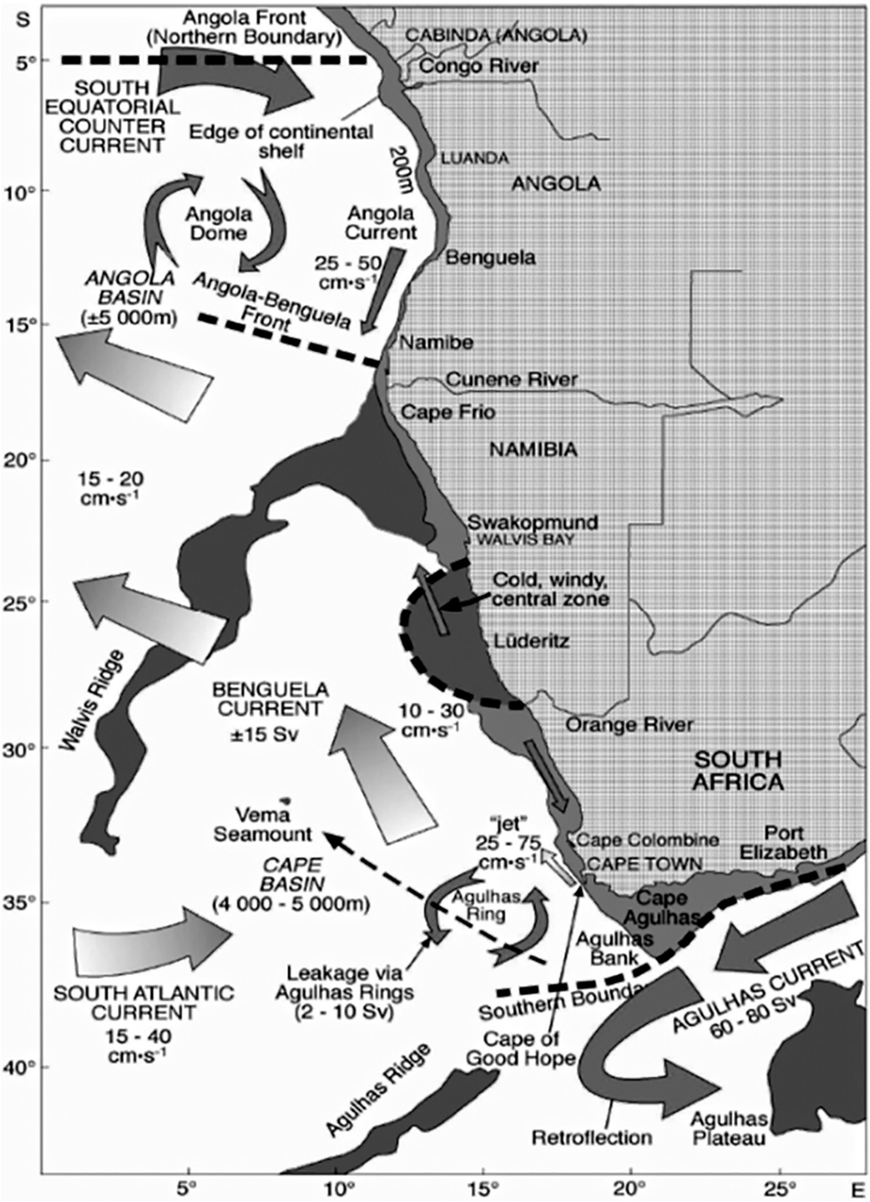

Figure 2 Map of the Benguela upwelling ecosystem showing positions of major coastal centres and dominant oceanographic features (BCLME, accessed from http://www.bclme.org).

The northern Benguela ecosystem is characterized by low concentrations of dissolved oxygen, especially in the north (Chapman & Shannon 1985). This is driven by a combination of factors including the southward movement of warm, oxygen-poor water in the Angola Current and the upwelling of low-oxygen water following upwelling at Cape Frio, as well as thermal stratification and the decay of *in situ* production (Monteiro & van der Plas 2006). While low-oxygen water can be found in the southern Benguela, its appearance is driven solely by the decay of *in situ* production (Monteiro & van der Plas 2006), and although it never approaches the areal extent witnessed off Namibia, its impacts in nearshore embayments may be significant (Pitcher et al. 2014).

Upwelled water is cold and nutrient-rich, and when introduced onto the shelf, it fuels massive phytoplankton production, especially downstream of upwelling centres (Shannon & Pillar 1986, Pitcher et al. 1992). Phytoplankton assemblages are initially dominated by diatoms, but these give way to dinoflagellates and smaller cells in space and time as nutrients are progressively stripped from surface waters (Pitcher et al. 1992). Periods of calm following upwelling events may lead to the outbreak of red tides, typically in enclosed embayments, which are particularly common during autumn in the south (Pitcher et al. 2014). Phytoplankton biomass tends to be greater in the northern than southern Benguela, owing to the more sluggish circulation there, although self-shading leads to lower production rates (Brown et al. 1991). Spring peaks in phytoplankton biomass are observed in both the southern (Hutchings et al. 2009) and northern (Louw et al. 2016) Benguela, although there is significant variability throughout the year.

Although the diversity of zooplankton assemblages in the Benguela ecosystem is typically low, and increases to the northern and southern boundaries of the system, biomass is high (Gibbons & Hutchings 1996). Zooplankton assemblages are dominated by large copepods and euphausiids (Hutchings et al. 1991), which tend to display ontogenetic diel vertical migration (DVM) and which have life cycles that take advantage of vertical changes in both cross-shelf water movement and the food environment (Pillar et al. 1992, Verheye et al. 1992). Most of the dominant copepods are herbivorous (Mauchline 1998, Verheye et al. 1992), whilst the euphausiids are omnivorous (Pillar et al. 1992). Seasonality in the biomass of zooplankton can be observed, and peaks in both the northern (Bode et al. 2014) and southern (Hutchings et al. 2009) Benguela may occur several months after that of phytoplankton. In the northern Benguela, zooplankton biomass peaks reflect the positions of the shelf break and the continental slope (Bode et al. 2014). Verheye et al. (1998, 2016) have noted long-term increases in the abundance of copepods in the southern and northern Benguela, respectively, over the period 1950–2010, which they attribute to a decrease in the biomass of pelagic fishes (see below).

Owing to its high productivity, the Benguela ecosystem supports valuable commercial fisheries for both pelagic and demersal species. Whilst the latter are more economically valuable, the former constitute the lion's share of the landings (FAO 2016). In the region, three species dominate the pelagic fish biomass: the sardine *Sardinops sagax* and the anchovy *Engraulis encrasicolis*, with the round herring *Etrumeus whiteheadii* coming in as a poor third (Roel & Armstrong 1991).

In common with other EBC systems, stocks of anchovy have tended to alternate with sardines as targets of the commercial fishery off South Africa (van der Lingen et al. 2006), in part reflecting bottom-up changes driven by climate and in part top-down changes driven by exploitation (van der Lingen et al. 2006). At present, sardine populations in the southern Benguela are estimated to be comparatively small and their centre of distribution has shifted eastwards (effectively) out of the Benguela (Watermeyer et al. 2016). However, sardines have historically comprised the major part of the pelagic fish fauna off Namibia (Shackleton 1987), where phytoplankton populations are enormous (Brown et al. 1991). At the end of the 1960s, the population size was estimated to be ~10 million t (Boyer 1996) and landings approached 1.5 million t, but following overexploitation, their populations crashed. It was thought, at the time, that anchovies and juvenile horse mackerel were direct competitors with sardines for resources and in an attempt to rebuild the sardine population, fisheries directed their efforts at the former species (Butterworth 1983, Shelton 1992). Unfortunately, however, this only resulted in the further decline of both anchovy and sardine populations: declines that to this day have not been reversed and the meagre quota is rarely filled (Mereghetti 2017).

Owing to the fact that small pelagic fishes occupy such a pivotal position in upwelling ecosystems, populations of some top predators off Namibia, especially seabirds, have declined to endangered levels (Crawford 2007, Crawford et al. 2008) in recent years. Fur seals (*Arctocephalus pusillus*) now regularly experience periods of starvation and mass mortality (Sibeene 2006). At the same time that small pelagic fish stocks collapsed, however, populations of bearded gobies (*Sufflogobius bibarbatus*) and jellyfish (see below) as well as horse mackerel (*Trachurus capensis*) have increased (Venter 1988, Boyer & Hampton 2001). Building on Bakun & Weeks (2006), Roux et al. (2013) have summarized these changes to the ecosystem, which are closely tied to increased flows of material and energy to the benthos, and which appear to be maintained by jellyfish.

Macromedusae

Species composition

Pagès et al. (1992) have detailed the medusozoans to be found within the Benguela upwelling ecosystem, and Pagès (1992), and Pagès & Gili (1991a, 1991b, 1992) have described cross-shelf, alongshore and vertical changes in assemblages and linked their observations to changes in the environment. The vast majority of the species are hydrozoans measuring less than 5 cm in diameter (Pagès et al. 1992).

Of the macromedusae considered here, seven Discomedusae, two cubozoans and one hydrozoan can be collected in the Benguela, and these are illustrated in Supplementary Figure 1. *Eupilema inexpectata* and an as yet undescribed species of *Drymonema* are restricted to the SW Cape; *Rhizostoma luteum* occurs in the nearshore waters of the Agulhas Bank and along the west coast of South Africa and into Namibia south of Lüderitz. This species is not generally very common in the Benguela, although it may occasionally be stranded in relatively high numbers at Groen River (30.83°S, 17.57°E; Supplementary Figure 2) and in smaller numbers at Lüderitz.

The cubozoan *Carybdea murrayana*, previously recognized as *Carybdea branchi* (Straehler-Pohl 2020), is common around Cape Town and is known to extend northwards as far Walvis Bay. It is seasonally abundant in very shallow waters and can be problematic for those swimming and diving in kelp beds. This species has never been caught in waters deeper than 50 m depth, although interestingly, the type specimen was recovered during the Challenger Expedition from waters off Sierra Leone, at a depth of 400 m. To our knowledge, there are no records of it being collected along the west coast of central Africa. *Chirodropus gorilla* is a large cubozoan that is routinely caught in pelagic and demersal trawls off Namibia, though never in abundance. Even though it is primarily an offshore species, it is regularly stranded during summer and autumn at Lüderitz in southern Namibia (sometimes in hundreds on one day: Grobler unpublished data), and occasionally also at Walvis Bay. This west African species is found from southern Namibia to the Gulf of Guinea.

None of the aforementioned species will be discussed further. All the remaining species of Discomedusae belong to the family Pelagiidae: *Chrysaora fulgida*, *Chrysaora africana*, *Chrysaora agulhensis* and *Pelagia noctiluca*. The hydrozoan is *Aequorea forskalea*.

Although *Chrysaora fulgida* had been synonymized with *Chrysaora hysoscella* by Pagès et al. (1992), it is regarded as a Benguela endemic, occurring from the western Agulhas Bank in the south to southern Angola in the north (Ras et al. 2020). *Chrysaora agulhensis* is a newly recognized species that is very closely related to *Chrysaora fulgida* (Ras et al. 2020); it is endemic to the Agulhas Bank and occurs from just north of Cape Town in the West to Port Elizabeth in the East (Figure 3A). Stiasny's (1939) arguments for considering that *Chrysaora africana* be synonymized with *Chrysaora fulgida* were long-held (Morandini and Marques 2010), but recent evidence suggests it is indeed distinct (Bayha et al. 2017, Ras et al. 2020). *Chrysaora africana* occurs from southern Namibia northwards to the Gulf of Guinea.

Pelagia noctiluca can be found around the entire region from Port Elizabeth in the SE to southern Angola in the NW (Figure 3B), whilst *Aequorea forskalea* occurs throughout the Benguela ecosystem (Pagès et al. 1992; Figure 3C, F): both species are regarded as having circumglobal distributions. Recent work suggests that local populations of *Pelagia noctiluca* are distinct from, and basal to, those in the North Atlantic and Mediterranean basins (Miller al. 2012), and elsewhere (Ale et al. 2019). The data presented by Ale et al. (2019) indicate that material from the SE Atlantic is more closely related to that from the SE Pacific (and not the North Atlantic), and they hint that it may not be *Pelagia noctiluca, sensu* Forskål. More taxonomic work is needed too on the identity of *Aequorea forskalea* (previously considered locally as *Aequorea aequorea*; Pagés et al. 1991), despite

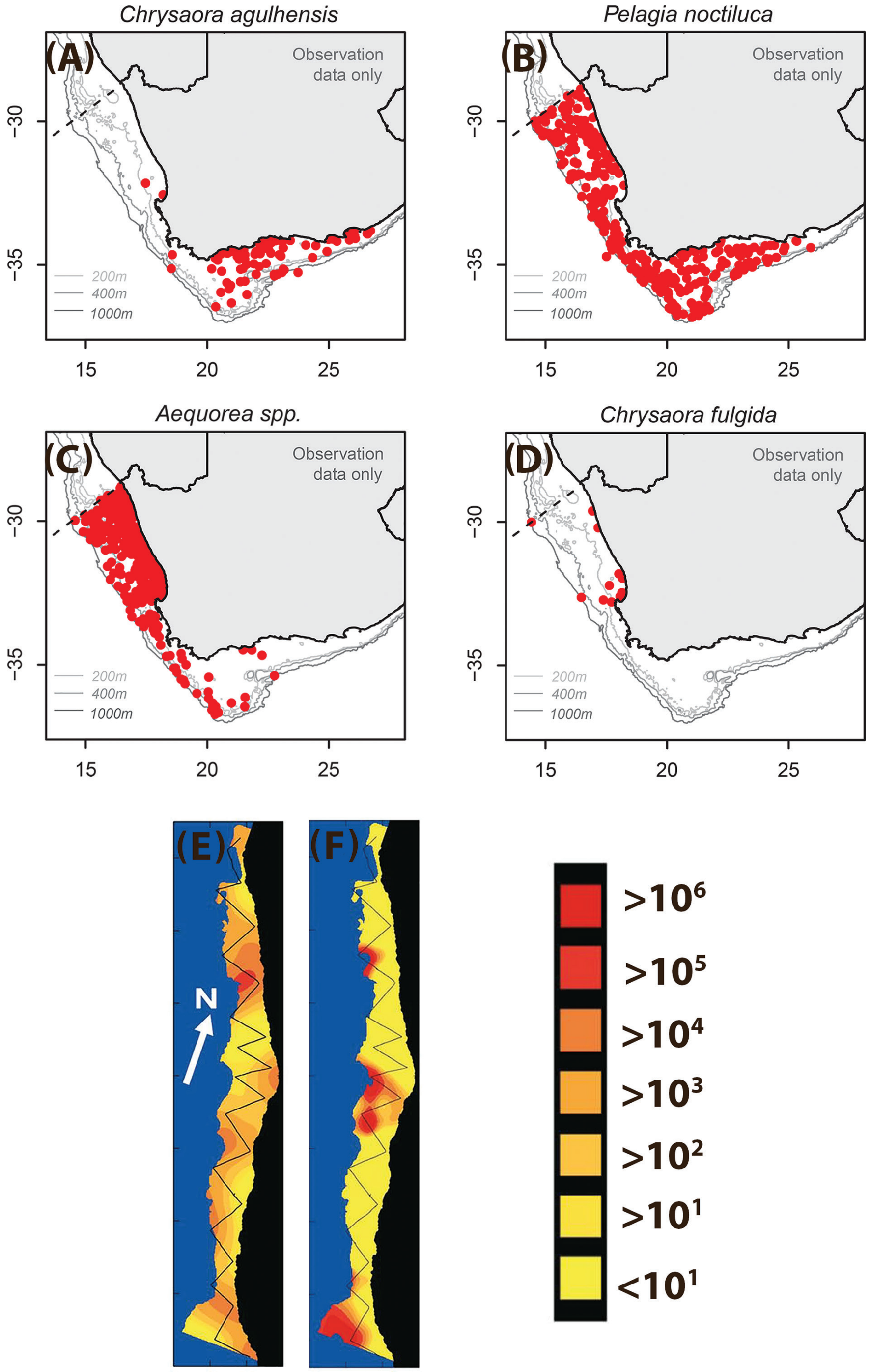

Figure 3 Distribution of *Chrysaora agulhensis* (A), *Pelagia noctiluca* (B), *Aequorea* sp. (C) and *Chrysaora fulgida* (D) from specimens collected by observers aboard eight annual research surveys conducted in South African national waters between January and May each year over the period 2011–2020. Data collected by SAEON Egagasini Biodiversity Unit in collaboration with the national Department of Forestry, Fisheries and Environment: Offshore Resources Research. Also shown is the distribution of *Chrysaora fulgida* (E) and *Aequorea* sp. (F) off Namibia in 2003 – colour scale is density, tonnes per nautical mile^2 (from Lynam et al. 2006).

the data of Dawson (2004: Figure 1, pp. 253), as the distribution maps for this species in WORMS exclude the Benguela region (Schuchert 2020).

Distribution

Space There are few data that describe in detail the distribution of *Chrysaora agulhensis* or of *Pelagia noctiluca*, over and above that provided above. Unpublished observations indicate that *Chrysaora africana* is thinly distributed in strictly coastal waters, but that it is regularly present in the harbour at Walvis Bay. Pelagic trawl catches from the RV Dr. Fridtjof Nansen show that *Chrysaora africana* can be found in very small numbers in more offshore waters of the northern Benguela to a depth of ~100 m and that it is more frequently encountered in the north of the region than elsewhere.

Most of our information about the distribution of macromedusae in the region applies to *Chrysaora fulgida* and to a lesser extent *Aequorea forskalea*: the dominant species in the (especially northern) Benguela ecosystem (Lynam et al. 2006). While both species are patchily distributed (Sparks et al. 2001) across the Namibian shelf and can be found together in pelagic trawl catches, their centres of abundance differ, with the latter tending to be found offshore (Fearon et al. 1992, Buecher et al. 2001, Sparks et al. 2001), and further north of the former (Fearon et al. 1992). Unpublished data collected by Grobler indicate that *Aequorea forskalea* is commonly recorded at Lüderitz, both stranded and in pelagic trawls, which agrees with the observations of Lynam et al. (2006; Figure 3F). In their two-year long study of gelatinous zooplankton in the Walvis Bay lagoon, Skrypzeck & Gibbons (2021) failed to collect any specimens of *Aequorea forskalea* (or any other species of *Aequorea*),[1] suggesting that polyps of this species are not located in shallow water, although *Chrysaora fulgida* was abundant. Differences in distribution of medusae may thus be linked, in part, to the distribution of polyps, although the two medusae clearly have differences in environmental optima, with *Aequorea forskalea* preferring warmer water than *Chrysaora fulgida* (Fearon et al. 1992, Sparks et al. 2001). That said, patterns may be reinforced by interspecific interactions (Sparks et al. 2001, Ras et al. 2020; see below). Results from data collected off Lüderitz during regular sampling of beach-stranded jellyfish (2008–2020) and during trawls conducted as part of oceanographic surveys (2008 to 2012) indicate that in southern Namibia, *Aequorea forskalea* is present off Lüderitz throughout much of the year (see below).

In their analysis of Namibian commercial and research catches over the period 1992–2006, Flynn et al. (2012) noted that the greatest numbers of jellyfish were observed at depths less than 200 m and between 20 and 24°S (Figure 4). It should be stressed that the data did not allow Flynn et al. (2012) to distinguish between species of jellyfish in their analyses, which were simply based on their presence or absence in trawl catches. The accumulation of jellyfish off Walvis Bay likely reflects the prevailing oceanography, which serves to concentrate, and retain, pelagic biota over the continental shelf there (Barange & Boyd 1992, Barange & Pillar 1992).

Unfortunately, similar information is not available for the southern Benguela, despite South Africa's more sophisticated economy and infrastructure. At the time of writing, jellyfish are not routinely recorded by either the commercial or research fishing fleets. That said, records of the incidence and identity of jellyfish in research catches have recently started to be collected in a project being driven not by the relevant fisheries department but by the Department of Science and Technology. Figure 3 provides a summary of this scant information to date, for the relevant species.

Information on cross-shelf changes in the size of *Aequorea forskalea* has not previously been reported. Off Lüderitz, however, the results from 17 midwater trawls conducted between 2008 and 2012 (covering all four seasons) suggest that juvenile *Aequorea forskalea* (<5 cm central disc diameter) tend to be found close inshore (62% of eight trawls at 2–5 nautical miles [nm] from shore) and rarely at 10 nm from shore (20% of five trawls), being entirely absent offshore (none were found in four trawls at 30 and 50 nm from shore: Figure 5A). Although these small size *Aequorea forskalea* generally contributed a small proportion (<15%) of the total sample size of most trawls, they

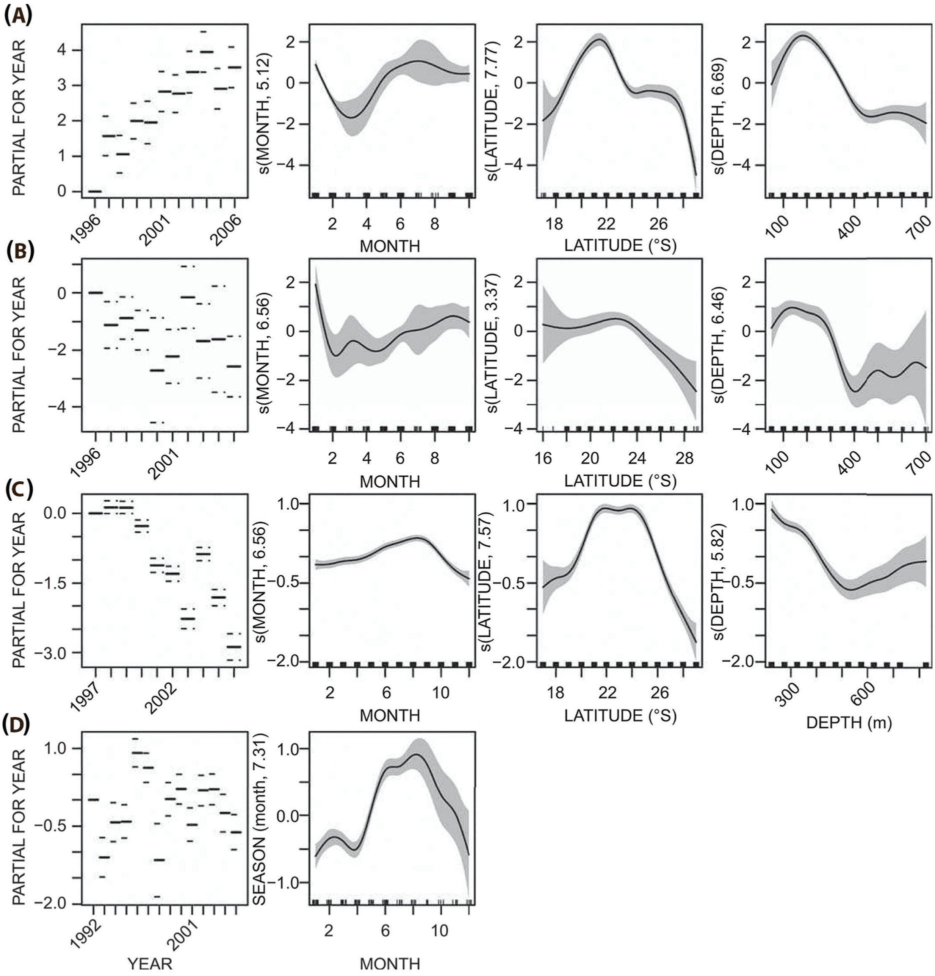

Figure 4 Term plots showing the response, the proportion of occurrence jellyfish, against predictors year, month (seasonality), latitude and depth for separate GAMs computed on jellyfish data collected off the coast on Namibia. Data from research cruises aboard the RV Dr. Fridtjof Nansen (1996–2006) 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 (from Flynn et al. 2012).

contributed 38% and 50%, respectively, to two trawls (September and July 2011) at 5 nm from shore. Small specimens of *Chrysaora fulgida* appear to be found inshore of large specimens in the northern Benguela (Fearon et al. 1992, Buecher et al. 2001). Unpublished data from the RV Dr. Fridtjof Nansen cruise conducted in August 2003 also indicate that smaller specimens of this species may be found off northern Namibia and that average size increases southward to Walvis Bay: an observation in agreement with that of Fearon et al. (1992).

Populations of both *Chrysaora fulgida* and *Aequorea forskalea* are primarily epipelagic (Flynn et al. 2012), certainly off Namibia, but individuals can be found throughout the water column (Flynn et al. 2012). Using data obtained from almost 40 submersible dives, Sparks et al. (2005) suggest that *Aequorea forskalea* might deepen their centre of abundance in the water column with increasing sea

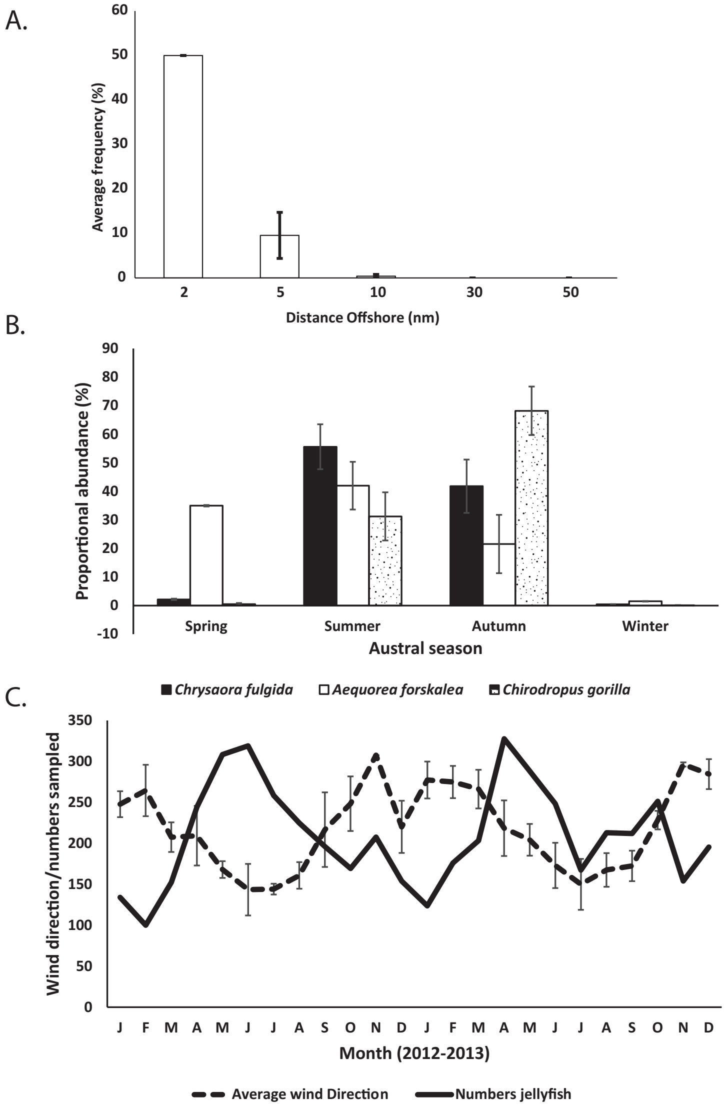

Figure 5 Average frequency (percent of catches; SE) of *Aequorea forskalea* measuring less than 5 cm bell diameter caught in midwater trawls off Lüderitz between 2008 and 2012 ($N = 17$), (A). Seasonality in the stranding of three species of regional macromedusae at Shearwater Bay, Lüderitz, based on routine observations of between 5 and 60 minutes duration (numbers dependant) collected daily from January 2014 to June 2020; data expressed as annual percentages (SE) (B). Number of stranded *Chrysaora fulgida* recorded (and sampled) each month during a 60-minute survey of Walvis Bay lagoon over the period January 2012–December 2013; average wind direction (SE) also shown from data collected using the AANDERAA anemometer at the Pelican Point lighthouse, measured at 10-inute intervals ($N = 17{,}544$; focal plane 35 m, measurement height to 39 m) (C).

surface temperature (SST), arguing that this could serve to limit offshore advection in the Ekman layer and thereby maintain themselves over the shelf. These authors supported this by indicating that individuals in nearshore waters have been found closer to the surface than they were further offshore (Sparks et al. 2005). *Aequorea forskalea* does not appear to demonstrate any size gradient with depth. However, in the case of *Chrysaora fulgida*, larger individuals are found in deeper than shallower water, offshore (Buecher et al. 2001).

Space-time Data regarding temporal changes in abundance of either *Chrysaora agulhensis* or *Pelagia noctiluca* are few. Unpublished data supplied by the community scientist Peter Southwood indicate that the latter is reported around Cape Town throughout the year, being most commonly found in winter. It is likely to be a mid-shelf species that gets moved into near coastal waters with changes in prevailing winds. As noted previously, personal observations indicate that medusae of *Chrysaora africana* are persistently present in small numbers off central Namibia. It is also been observed at Lüderitz, albeit rarely, and 26 specimens were recovered stranded on 14 of 624 sampled occasions between 2011 and 2016; all were immature, with an average diameter of 11.2 cm (±2.8 cm standard deviation), and all but one specimen were recovered in summer and autumn (Grobler unpublished data).

Information on interannual changes in the distribution or biomass of jellyfish in the region is restricted, and certainly nothing exists for the southern Benguela. Whilst there is no pattern of consistent change in the populations off Namibia in recent time (Flynn et al. 2012; Figure 4), there do appear to have been increases since the early 1970s, despite the lack of hard baseline data. Venter (1988) makes the first reference to this increase stating “The abundant occurrence and wide distribution of jellyfish off the coast of South West Africa (Namibia) is a well-known phenomenon, especially after the dramatic decrease in pelagic fishing in 1972” Venter 1988, pp. 56). As Fearon et al. (1992) noted and Roux et al. (2013) stressed, if jellyfish were as common prior to the early 1970s as they are now, they should have been reported in the otherwise comprehensive studies of Hart & Currie (1960) or Stander & De Decker (1969), but they were not, implying that they were not a major component of the system at that time. Ephyrae of *Chrysaora fulgida* dominate gelatinous zooplankton communities in Walvis Bay lagoon (Skrypzeck & Gibbons 2021). However, NONE were caught, or at least reported upon, by Unterüberbacher (1964) “from the regular plankton collections made in Walvis Bay over the period 1959–1962, though he did note the presence of other, similarly sized jellyfish in his samples…[again suggesting]…that large jellyfish populations were not a feature off Namibia at the time” (Skrypzeck & Gibbons 2021, pp. 10).

On the intra-annual scale, jellyfish are reported throughout the year in the northern Benguela (Venter 1988, Fearon et al. 1992), but appear to peak in abundance over the shelf during late winter through to mid spring (Flynn et al. 2012; Figure 4). We should be cautious in our interpretation of the latter, because they could reflect processes of physical aggregation linked to seasonal oceanographic forcing (Barange & Boyd 1992, Barange and Pillar 1992), rather than population processes *per se* (Graham et al. 2001), especially given that most of the data were collected over the shelf.

Unpublished data show that *Chrysaora fulgida* can be found throughout the year in the shallow waters off Walvis Bay and Lüderitz (Figure 5B, C). This species is more commonly stranded at Lüderitz between late spring and early autumn, with the highest numbers usually found during the period December to March. Although it is rarely present on beaches during winter and early spring (June – October) (Figure 5B), it can be caught during inshore trawl surveys off Lüderitz at that time, indicating that the species is present throughout the year along the southern part of Namibia’s coast too. The data from Walvis Bay indicate that the presence of large medusae may be related to prevailing winds from the SE and that westerlies are associated with reduced numbers (Figure 5C). Unpublished data collected from Lüderitz by Grobler indicate that most jellyfish strandings there are also linked to coastal winds from the SW. These observations suggest that their (inshore) presence may be linked to upwelling and tentative support for this comes from new evidence provided by Skrypzeck et al. (2021) using stable isotopes of $\delta^{15}N$ and $\delta^{13}C$ (Figure 6). These authors show that the $\delta^{15}N$ signatures of the large, sexually mature medusae encountered in Walvis Bay lagoon are lower than those of ephyrae and small medusae, but are statistically indistinguishable from large specimens collected offshore (Figure 6). The high $\delta^{15}N$ of inshore specimens is matched by primary producers there with very different $\delta^{13}C$ values (macroalgae and marine angiosperms), suggesting a reliance by production on new nitrogen: offshore populations being sustained by recycled nitrogen (Skrypzeck et al. 2021).

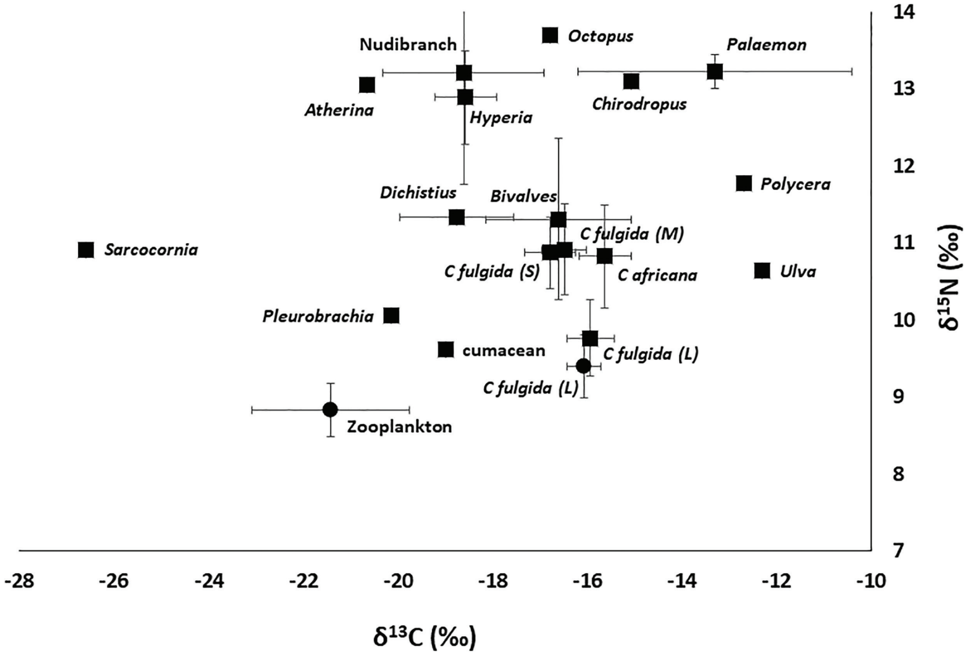

Figure 6 Isotopic biplot (δ^{13}C and δ^{15}N, mean values ±95% confidence intervals) of organisms collected in Walvis Bay (circles), and waters further offshore (squares). Data for *Chrysaora fulgida* subdivided by size class: L ≥300 mm, M <300 mm, ≥100 mm; S <100 mm. From Skrypzeck et al. (2021).

Although there are no data regarding the structure of populations in the case of *Aequorea forskalea*, those of *Chrysaora fulgida* appear to comprise a wide size range of individuals throughout the year (Buecher et al. 2001; Figure 7A). That said, proportionally more small individuals are recovered during summer than winter (Buecher et al. 2001). Although the data on which these observations are based were derived from area-integrated trawl catches taken at depths greater than 50 m (Buecher et al. 2001), they are supported, in part, by measurements of randomly sampled individuals ($n = 5508$) collected in Walvis Bay lagoon at approximately bi-weekly intervals over the period January 2012 to February 2014 (Figure 7B). Although all size classes were represented during spring and summer, small (<20 cm diameter) individuals dominated the samples (see "Reproduction" section, below) and larger individuals (>50 cm diameter) were missing in autumn and winter (Figure 7B). Off Lüderitz, populations of stranded *Chrysaora fulgida* included both juveniles and adults during all months when they were found on beaches (Figure 7C), but the largest contribution by juveniles <15 cm diameter occurred between summer and autumn (December to April).

Quantitative information on temporal changes in the abundance or distribution of either *Aequorea forskalea* or *Chrysaora fulgida* in the southern Benguela is entirely missing. That said, populations of the latter species may become more obvious in nearshore waters during autumn, as dense aggregations have forced the temporary shutdown of Koeberg nuclear power station just north of Cape Town during May 2005 and March 2020 (see below).

There is no firm evidence to indicate that either species displays DVM (Flynn et al. 2012), although no detailed studies using tags have been undertaken (as Fossette et al. 2016).

Biomass, growth and mortality

Biomass For reference purposes, information on the relationships between bell diameter and mass and other gross morphological variables of the common medusae found in the Benguela Current

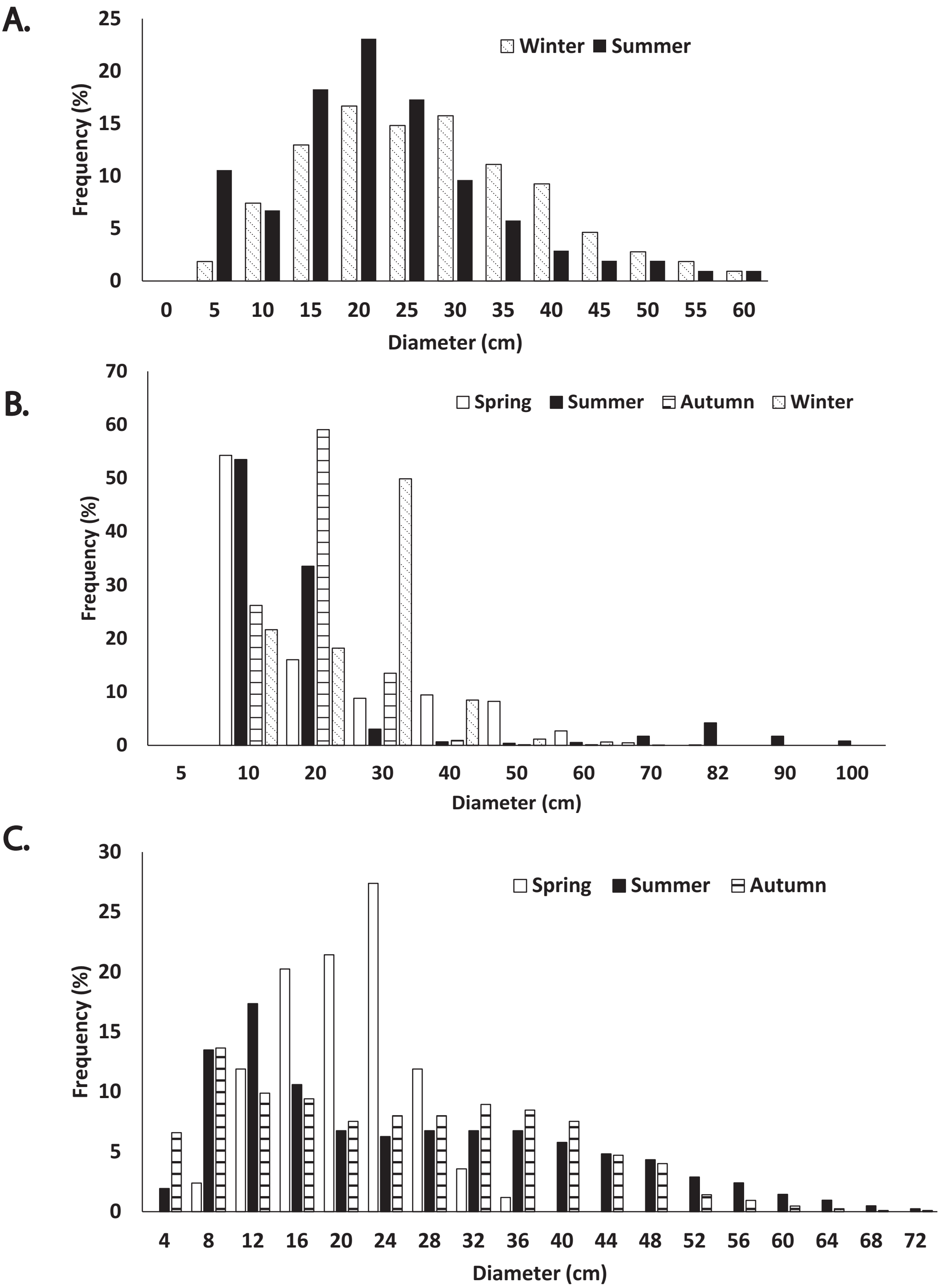

Figure 7 Seasonal changes in the size distribution of *Chrysaora fulgida* sampled in waters offshore of Walvis Bay (A) and in Walvis Bay lagoon (B), and stranded on the lagoon beaches at Lüderitz (C). Data in (A) from Buecher et al. (2001) and data in (B, C) from samples measured during the sampling of stranded material as described in Figure 5 (above).

system are shown in Supplementary Table 1. Information on carbon and nitrogen content of different tissues can be found in Supplementary Table 2.

Unfortunately, there are no empirical estimates of jellyfish biomass in the southern Benguela and the few we have from the northern sub-region vary significantly with the method of data collection. The South West Africa Pelagic Egg and Larvae Surveys (SWAPELSs) were conducted over the period January 1982 to February 1989 and comprised a series of routine stations extending latitudinally from 17°30′S to ~29°S, and offshore to a distance of 65 nm. Paired Bongo nets with a mouth opening of 57 cm diameter, fitted with 300 and 500 μm meshes, were used to collect zooplankton samples in the upper 50 m, and although they were not specifically designed to target jellyfish, the latter were nevertheless captured. Using these data, Fearon et al. (1992) estimated that the average biomass of jellyfish off Namibia during the 1980s was 40.5 million t: 10.8 million t *Aequorea forskalea* and 29.7 million t *Chrysaora fulgida*. Fearon et al.'s (1992) estimates were generated by extrapolation and using line-integration methods and were accompanied by estimates of standard error and coefficient of variation. The latter ranged between 0.42 and 0.46 for *Chrysaora fulgid*a and *Aeqourea forskalea*, respectively, and 0.33 overall. There was significant intra-annual and inter-annual variability in estimates, which also changed latitudinally (Fearon et al. 1992).

Plankton nets are not an ideal method for collecting information on the biomass of relatively large animals. Using data collected from pelagic fishing trawls and applying the swept area methods, Sparks et al. (2001) estimated that there were 4.9 million t of jellyfish off Namibia from a survey conducted off Walvis Bay during winter 1999. This total was broken down as 3.1 million t of *Aequorea forskalea* and 1.8 million t of *Chrysaora fulgida*. The data used by Sparks et al. (2001) were collected along a **single** cross-shelf transect, and mean data were scaled up to the total shelf area (179,000 km^2), assuming both species were homogeneously distributed. No estimates of variation were provided. The greater relative biomass of *Aequorea forskalea* than *Chrysaora fulgida* estimated by Sparks et al. (2001) contrasts with the findings of Fearon et al. (1992), which reflects (in part) differences in the location of the sampling areas.

Although large fishing nets are a better tool for sampling large jellyfish than small plankton nets and have been widely employed elsewhere to determine jellyfish biomass (e.g. Brodeur et al. 2008a), it needs to be remembered that small individuals will pass through meshes, while larger animals may get extruded owing to their gelatinous nature. Multi-frequency hydroacoustics can be used to quickly assess the biomass of pelagic organisms over large areas, if appropriate target strengths have been determined and discriminatory algorithms have been developed. Brierley et al. (2001) pioneered the use of this tool in the region using vessel-mounted echosounders at 18, 38 and 120 kHz during an experimental survey on board the RV DR. FRIDTJOF NANSEN in 1999. These authors were able to distinguish targets attributable to *Chrysaora fulgida* and *Aequorea forskalea*, suggesting that "a simple multifrequency approach…could be used to discriminate between echoes from jellyfish and some commercially important pelagic fish" (Brierley et al. 2001, pp. 55). The multi-frequency hydroacoustic tool was further improved during another experimental campaign in 2001: an additional transducer (200 kHz) was added to the echosounder, studies on single jellyfish targets of different sizes were conducted, and issues around zooplankton backscatter were corrected (Brierley et al. 2004, 2005). Finally, during August 2003, a shelf-wide survey was conducted that was aimed specifically at determining jellyfish biomass, and Lynam et al. (2006) published the results in a widely cited paper. It was estimated that (in 2003), "the biomass of jellyfish was 12.2 million t (99% by mass *Aequorea forskalea*, mean jellyfish density 361 t·nm^{-2}, standard error 22 t·nm^{-2}), and that the total biomass of fish was 3.6 million t (Cape horse mackerel 1.1 million t, mean 33 t·nm^{-2}, SE 1.5 t·nm^{-2}; Cape hake 1.7 million t, mean 50 t·nm^{-2}, SE 2.3 t·nm^{-2}; clupeoids 0.8 million t, mean 23 t·nm^{-2}, SE 1.0 t·nm^{-2})" (Lynam et al. 2006, R493). Unfortunately, the 2003 survey has not been repeated, primarily because regional fisheries vessels lack the echosounders, expertize and budget needed.

Table 2 Von Bertalanffy growth parameters *of Chrysaora fulgida* and *Aequorea forskalea* in the northern Benguela ecosystem

Species	*n*	$L_{\min}$ (cm)	$L_{\max}$ (cm)	L_∞ (cm)	W_∞ (g)	K (yr^{-1})	C	M
Aequorea forskalea	3396	4	10	11.1	141	0.87	0.50	2.09
Chrysaora fulgida	2240	7.5	62.5	68.2	10 725	4.30	0.25	4.83

Source: From Palomares and Pauly (2009).

Growth, mortality and longevity There are no empirical estimates of growth rate or mortality for any species of medusae within the Benguela ecosystem. However, using the length frequency data published by Brierley et al. (2001) and Buecher et al. (2001), Palomares & Pauly (2009) derived estimates for these parameters for *Chrysaora fulgida* and *Aequorea forskalea* (Table 2) using a variety of methods, including Wetherall plots (Wetherall 1986). These authors adjusted the von Bertalanffy growth curve parameters to account for seasonality, following Somers (1988), by setting the winter point as July (Palomares & Pauly 2009). The winter point represents the month when water temperatures are lowest and growth is assumed to be at its minimum: it determines the timing of the first sinusoidal growth oscillation. As Palomares & Pauly (2009) stress, the use of Wetherall plots does not generate values of mortality (Z, where $Z = M$, as $F = 0$: Z = total mortality, F = fisheries mortality and M = natural mortality), but rather values of mortality relative to K (growth coefficient) which should be considered heuristic.

The estimates of L_∞ (maximum size) derived by Palomares & Pauly (2009) for *Chrysaora fulgida* are some 12 cm smaller than the maximum size observed in the field, where W_∞ (maximum weight) may exceed 20 kg (unpublished data). Whilst Pagés et al. (1991) recorded specimens of *Aequorea forskalea* with a maximum diameter of 27.5 cm, which differs by about 16 cm from the L_∞ derived of Palomares & Pauly (2009), this discrepancy likely reflects differences in the measures used. The latter authors used the diameter of the thickened central lens, which gets recovered from trawls and which was recorded by Buecher et al. (2001) and Brierley et al. (2001), whilst the measurements of Pagés et al. (1991) also included the more delicate marginal umbrella. Brierley et al. (2004) calculated that the relationship between central lens and total diameters (Supplementary Table 1B), and if the L_∞ value estimated by Palomares & Pauly (2009) is so adjusted, material differences with the observations of Pagés et al. (1991) disappear.

Attempts to age Discomedusae from field specimens are fraught. Size is an unreliable indicator of age, given that individuals may grow rapidly when provided with abundant food at optimum temperatures, but will shrink (not starve to death) when environmental conditions deteriorate (Arai 1997). The statoliths of cubozoans can be used to age individuals, in much the same way that otoliths can be used to estimate the age of bony fish, owing to the fact that the basanite crystals (calcium sulphate hemihydrate) are consolidated (e.g. Heins et al. 2018). Statoliths are sectioned and polished and then (daily) rings counted using light or scanning electron microscopy (e.g. Gordon & Seymour 2012). In the case of scyphozoans, however, the statoliths comprise a loose accumulation of individual crystals (Heins et al. 2018 and references therein), which makes ageing outside controlled experimental environments difficult. The maximum age of *Chrysaora fulgida* in captivity exceeds 18 months.

Beach-stranded material at Lüderitz suggests that cohort progression could perhaps be used to analyse the growth of juvenile *Chrysaora fulgida* (Figure 8). Although caution should be exercized in the interpretation of these data, preliminary results of the two cohorts that were observed over the period February–March 2011, indicate that growth rates were similar in each (Figure 8) and that they were rapid.

Reproduction

Sexual reproduction No studies on the reproduction of *Pelagia noctiluca* or *Aequorea forskalea* have been conducted in the region. *Pelagia noctiluca* in the central and northern Adriatic Sea and

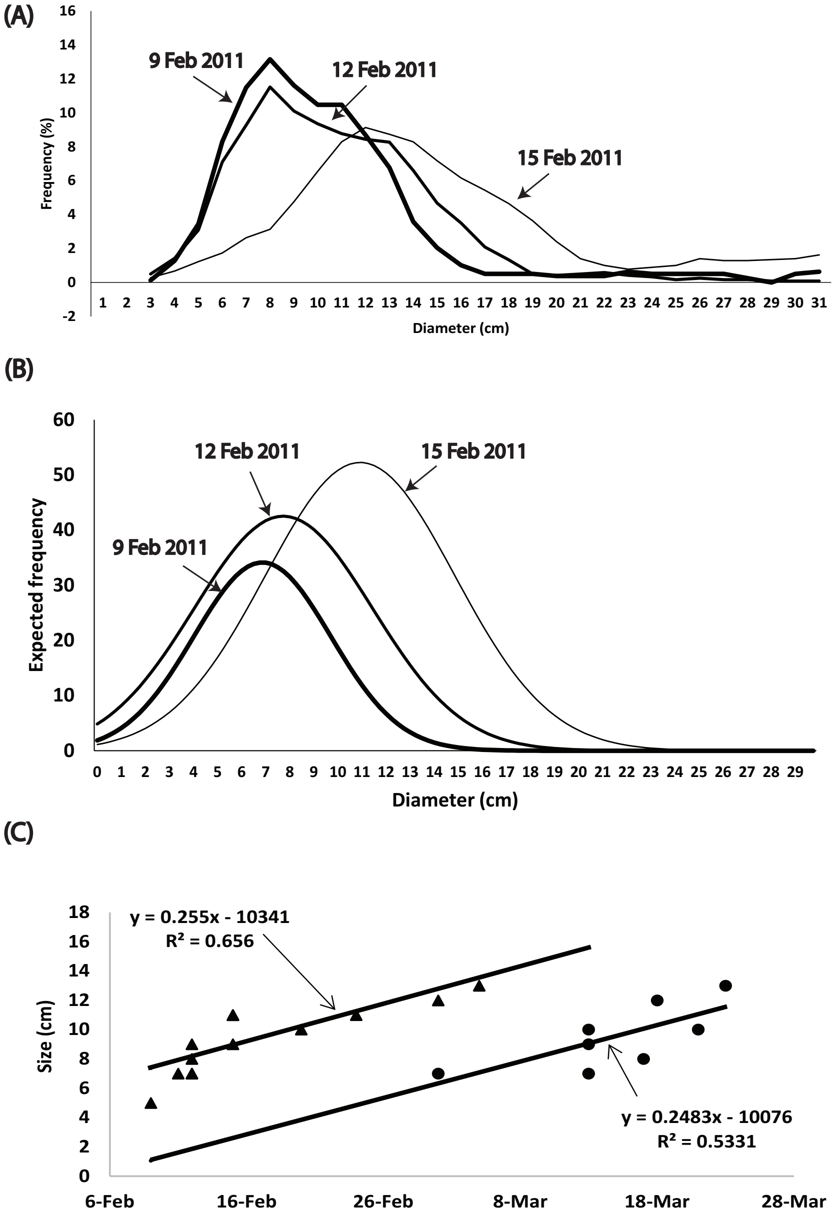

Figure 8 The size structure of beach-stranded specimens of *Chrysaora fulgida* at Lüderitz lagoon observed on three occasions over the period 9–15 February 2011 (A); changes in the average size of stranded *Chrysaora fulgida* from two cohorts measured in Lüderitz lagoon during February and March 2011 (B). Data are random samples of stranded jellyfish (Grobler unpublished).

in the Strait of Messina appear to reproduce throughout the year as oocytes of all maturity states can be found each month (Rottini Sandrini & Avian 1991, Milisenda et al. 2018). This contrasts with the situation in the North Atlantic (Russell 1970).

While there is little information regarding reproduction in *Chrysaora agulhensis*, like *Chrysaora fulgida* and *Chrysaora africana*, the species is known to be dioecious (Ras et al. 2020). Unfortunately, the sex of an individual *Chrysaora* from the region can only be determined by histological examination. Our knowledge of the sex ratios in populations of any species of *Chrysaora* (or indeed any Discomedusae for that matter) is almost entirely missing, although detailed observations conducted in Walvis Bay suggest that the sex ratio for *Chrysaora fulgida* there is ~1:1 (F:M) (Skrypzeck 2019).

Our understanding of gonad development and reproductive maturity of macromedusae in the Benguela ecosystem is entirely restricted to *Chrysaora fulgida* and to a lesser extent *Chrysaora africana*.[2] From the work recently conducted in Walvis Bay (Skrypzeck 2019), it would appear that the pattern of gametogenesis in both the species is similar to that displayed by other Discomedusae (Eckelbarger & Larson 1988, Eckelbarger 1994, Schiariti et al. 2012). Synchronous oocyte development is observed in *Chrysaora fulgida* and group-synchronous development in *Chrysaora africana*. The oocytes of *Chrysaora africana* are slightly smaller than those of *Chrysaora fulgida*, and they have a slightly different shape. The gonads of both species appear to have specialized gastrodermal structures (less conspicuous in *Chrysaora africana*), and there is a close association between the developing oocytes and the gastrodermis (Skrypzeck 2019).

Reproduction of *Chrysaora fulgida*, at the population level, occurs throughout the year: it appears to be aseasonal, at least for some parts of the population. Whilst individuals may mature at a relatively small diameter (M 22.5 cm; F 36 cm), they may also only mature at a larger size (up to M 73.4 cm; F 77 cm). Populations off central Namibia therefore appear to display reproductive heterogeneity, with individuals dancing to their own rhythm. Off Walvis Bay, sex-indeterminable medusae of *Chrysaora fulgida* dominate nearshore samples throughout the year and sexually mature medusae are relatively uncommon (see Figure 9A, Table 3). By contrast, off Lüderitz in southern Namibia, the majority of adult *Chrysaora fulgida* stranded in late summer and autumn have well-developed gonads, which indicates that some parts of the population may display reproductive seasonality. Histological evidence suggests that individuals are semelparous, although there is the possibility that some females may spawn over a protracted period: a partially spent individual (~38 cm diameter) has been observed.

Chrysaora africana seems to mature at ~20 cm diameter, and reproduction at the population level appears to be strongly seasonal, with a peak in autumn and winter (Figure 9B, Table 3). Females seem to be able to reproduce in a serial fashion over a more protracted period of time before dying: individuals display restricted iteroparity (Skrypzeck 2019). Most of the *Chrysaora africana* recorded in the nearshore waters of Walvis Bay are mature, although immature individuals can be found in all seasons (Skrypzeck 2019).

Asexual reproduction While *Pelagia noctiluca* is holoplanktonic, and so produces no polyps, the balance of species is metagenic. That said, no polyps of any Discomedusae have ever been observed *in situ* in the Benguela region. However, it is likely that they will be attached to hard substrata (Lucas et al. 2012), which for the most part occur in shallow water (Rogers & Bremner 1991). However, the benthic polyps of both *Chrysaora africana* and *Chrysaora fulgida* have been described from cultures (Ras et al. 2020), and they essentially resemble others of the genus (Morandini & Marques 2010). Ziegler & Gibbons (2018) noted that asexual reproduction in the polyps of *Chrysaora fulgida* includes lateral budding by means of stolons, the production of podocysts,[3] strobilation (see below) and lateral budding (*sensu* Adler & Jarms 2009). The latter of these methods was the most prevalent way by which new polyps were generated, and although most polyps produced lateral stolons, few of these developed buds (Ziegler & Gibbons 2018). Asexual polyp production appears to be positively impacted by food (concentration and feeding frequency) and temperature over the range 12–20°C (Ziegler & Gibbons 2018). Although podocysts were formed in low numbers at all temperatures, more were produced at lower than higher food densities; no podocysts were produced by starved polyps (Ziegler & Gibbons 2018).

To return to the medusa phase of the life cycle, the asexual polyp, under species specific environmental conditions of food, temperature and/or salinity, will undertake the process of strobilation to release ephyrae (Raskoff 2003, Treible & Condon 2019). Strobilation by polyps of *Chrysaora*

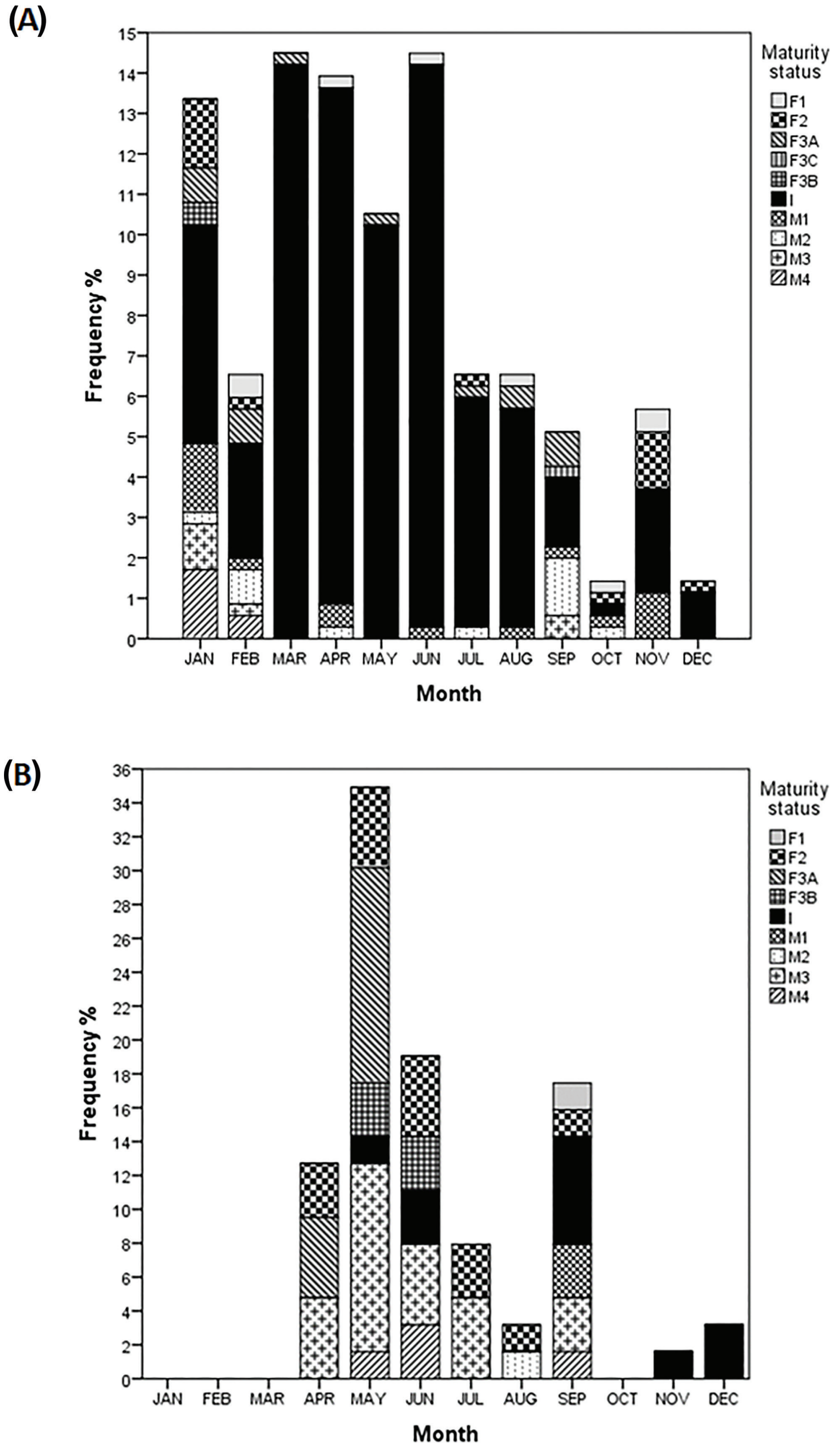

Figure 9 The average frequency (%) of different gonad maturity statuses of female (F1–F3C), sex-indeterminable (I) and male (M1–M4) *Chrysaora fulgida* and *Chrysaora africana* among stranded medusae at Walvis Bay; January 2012–February 2014. See Figure 6 for details of sampling, and Table 3 for information on maturity status descriptions (adapted from Skrypzeck 2019).

Table 3 Description of the maturity statuses of *Chrysaora africana and Chrysaora fulgida*, as determined from histological measurements of specimens caught in Walvis Bay lagoon (adapted from Skrypzeck 2019).

Maturity Status	Description
I	Sex-indeterminable, no gonad development
F1	Unripe female, predominance of ≥50% pre-vitellogenic oocytes
F2	Unripe female, predominance of >50% early vitellogenic oocytes to mid vitellogenic oocytes and <15% of late vitellogenic to released stage oocytes
F3	Ripe female, ≥15% of late vitellogenic to released stage oocytes. To be categorized into - • Ripe/ovulating gonad **(F3A)**, or • Disintegration of gonad structures **(F3B)**, or • Partially spent gonad **(F3C)**
M1	Unripe male, <70% of sperm follicles contains spermatozoa
Mripe	Ripe male, ≥70% of sperm follicles contains spermatozoa. To be categorized into -: • Individual sperm follicles visible that contains spermatozoa **(M2)**, or • Sperm follicles clustered or merged, spermatozoa may or may not be released into subgenital sinus, and/or sperm follicles merged into highly condensed spermatozoa areas **(M3)**, or • The disintegration of follicle walls, gastrodermis and subgenital sinus **(M4)**

fulgida was observed by Ziegler & Gibbons (2018) in the laboratory, but only rarely and only at 12°C. The number of ephyral discs produced ranged from five to eight (Ziegler & Gibbons 2018). We should be cautious in our treatment of these data because the experiments were only conducted for a period of 30 days under a constant set of environmental conditions; strobilation was not the subject of the study. More extensive but hitherto unpublished work by Krish Lewis at the Two Ocean's Aquarium demonstrates that polyps of *Chrysaora fulgida* can be readily maintained at temperatures between 12 and 20°C, but that strobilation is stimulated when polyps are exposed to a temperature of 11°C for a period of 14 days, after which the temperature is raised to 14°C (fed to satiation daily, under 12-hour light). Under these conditions, up to 42 ephyral discs per polyp may be observed (average 30) and individuals may re-strobilate at a reduced rate some four to six weeks later. By contrast, strobilation of *Chrysaora agulhensis* is achieved when the temperature is raised from a two-week exposure at 14°C, to 18–20°C, the number of ephyrae in this case averaging 23 per polyp (29 maximum) (Krish Lewis, Two Oceans Aquarium; unpublished data).

Skrypzeck (2019) has recently detailed the morphology and development of the ephyrae of *Chrysaora fulgida* and *Chrysaora africana* from field collections in Walvis Bay lagoon, noting that the two species are readily distinguishable *in situ*. These observations imply that the polyps of both species are present in the immediate area, perhaps on the infrastructure associated with the industrial harbour there, or with associated maritime activities (Skrypzeck 2019). Using these descriptions, Skrypzeck & Gibbons (2021) chronicled the structure of gelatinous zooplankton assemblages over the period January 2012 to December 2013, changes in which appear to be driven primarily by bottom temperature and day length.

The data presented by Skrypzeck & Gibbons (2021) indicate that ephyrae of *Chrysaora africana* may appear in the water column as early as mid-June and persist until early October, but peak in abundance at the end of winter (August). In the case of *Chrysaora fulgida*, newly released ephyrae also first make an appearance in the plankton during mid-winter (July), soon after the lowest bottom temperatures are recorded. They peak in abundance in late winter and spring (August/September/October) and have disappeared by the start of summer (December) (Figure 10A). While more developed ephyrae first occur in the water column at the end of winter (August) and have all but vanished by mid-summer (January), they may make periodic appearances during late summer (February to May) as juveniles. In other words, the recruitment of ephyrae to the plankton off Walvis Bay is not continuous throughout the year, but is a protracted six-month affair.

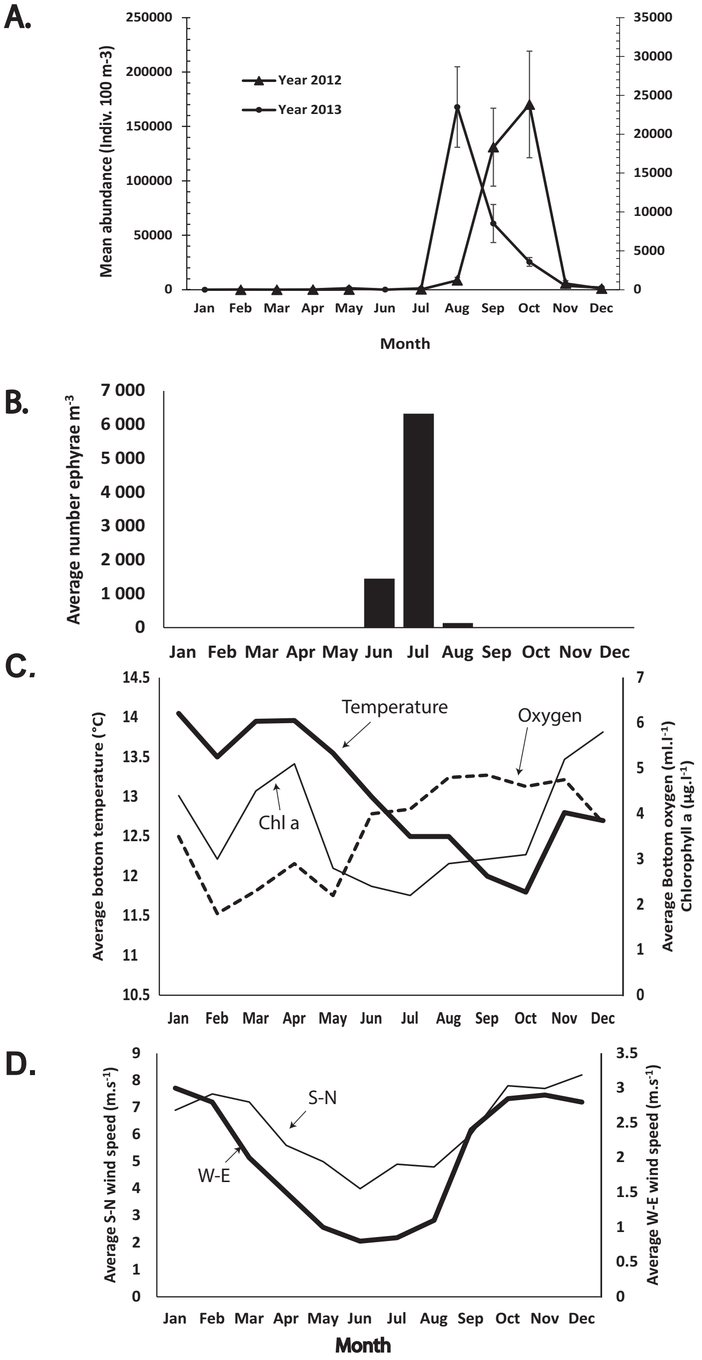

Figure 10 Average monthly abundance (SE) of ephyrae of *Chrysaora fulgida* in Walvis Bay lagoon during 2012 (left *y*-axis) and 2013 (right *y*-axis) (A); monthly average number of ephyrae m^{-3} at three inshore stations at Lüderitz, collected as part of zooplankton samples during routine oceanographic surveys (B), with accompanying environmental data (C, D). Data in B - D derived from hourly (wind speeds) or weekly (ephyrae, oxygen Chl a) observations averaged across months and years, 2010–2013, ephyrae; 2010–2018, bottom temperature and oxygen; 2008–2017, Chl a; 2011–2017 wind speeds). (A) from data in Skrypzeck & Gibbons (2021), (B - D) from Grobler (unpublished).

Interestingly, it would appear from unpublished data that ephyrae of *Chrysaora fulgida* may first appear in the water column at Lüderitz during April and persist only until September (Figure 10B) (Grobler unpublished data). In other words, the release period at ~26°S is some two months in advance of that at ~23°S (Walvis Bay), although again it may occur over a protracted period of time. The nine-year time series of data collected in the inshore waters of Lüderitz (only a part of which is shown in Figure 10B) indicates that ephyrae are most abundant during winter (when upwelling winds off Lüderitz are weakest), and are least common during spring and summer (October to February), when upwelling winds are strongest (Figure 10D). This is unlike the situation at Walvis Bay, where the strongest upwelling winds occur during September. Ephyrae were most prevalent at Lüderitz when bottom water temperatures were in the range 11–12.6°C (though they were seen in waters at 14°C or more) and when bottom dissolved oxygen levels were high (between 3 and 6 $mL \cdot L^{-1}$) (Figure 10C). Winter periods off Lüderitz are also characterized by frequent storms and high swell conditions, with increased turbulence and sediment loads in the water column. Thus, the highest abundance of ephyrae in the inshore waters of Lüderitz occurs under the combined conditions of lowest upwelling strength, high bottom dissolved oxygen, low bottom temperatures and increased turbulence (due to high winter swells).

While ephyrae of Discomedusae are rarely encountered in plankton samples from the southern Benguela, Helm and Gibbons (2008) did note what appear to be ephyrae of *Chrysaora* between St. Helena Bay and Lambert's Bay during spring 2000. Unfortunately, because zooplankton samples are not collected regularly around South Africa, it is not possible to comment further. That said, the data demonstrate that polyps are present in the region and, given that bottom water temperatures are coldest off the west coast of South Africa during spring (Shannon 1985), they imply that strobilation is probably initiated as elsewhere.

The data provided by Skrypzeck & Gibbons (2021) indicate that Stage 0 and Stage 1 ephyrae[4] of *Chrysaora fulgida* appear together in plankton samples in the lagoon at Walvis Bay (July), suggesting that there is a very short development period from the former to the latter. Stage 2 ephyrae appear for the first time in August and persist until December, implying a development time of approximately one month from Stage 0 to Stage 2 (total body diameter 2.07 ± 0.48 mm – 14.24 ± 4.03 mm), at an ambient temperature of 13.2°C. "Interpretation of [the] data with regard to subsequent ephyral development is complicated by the fact that the more advanced stages (Stage 3–5) were pooled and recorded in samples throughout the year, albeit at very low densities. Two hypotheses can be invoked to explain this observation: (1) small numbers of polyps may be strobilating throughout the year, either inside or outside the lagoon, (2) the further development of ephyrae within Walvis Bay lagoon is variable and potentially slow. Neither of these can be discounted but as there appear to be two peaks in relative abundance of the older stages (Stage 3–5) each year (late winter and early spring; autumn), it is possible that ephyrae released early in the season mature quickly, whilst those released at the end develop more slowly. This is not unlikely given that growth rates of ephyrae will vary with the quantitative and qualitative food environment (e.g. Båmstedt et al. 2001), as well as with temperature (e.g. Widmer 2005)" (Skrypzeck & Gibbons 2021, p. 80).

The densities of Stage 0, and especially Stage 1, ephyrae of *Chrysaora fulgida* recorded in the lagoon at Walvis Bay by Skrypzeck & Gibbons (2021) were exceedingly high: maximum densities of Stage 1 ephyrae greater than 4672 m^{-3} were observed in one sample collected during October 2012. By contrast, the densities of the more advanced stages (Stage 3–5) only attained a maximum of 8 m^{-3}, again collected during October 2012. Two things become obvious from these data. First, despite its lagoonal nature (Skrypzeck & Gibbons 2021), advection to the outside, nearshore environment is effective. And second, given that the densities observed are higher than those that have been observed for any other species of jellyfish to date, potential contributions to adult populations are enormous, in the absence of mortality.

Interactions with other species and human activities

Diet

There has only been one explicit and published study on the diet of macromedusae in the Benguela region and that is of *Chrysaora fulgida* in the Walvis Bay lagoon (Flynn & Gibbons 2007). The data presented by the latter authors should be treated with some level of caution as only 55 individuals were examined; they were caught using a fine mesh dip net at the surface in September 2003 (Flynn & Gibbons 2007). The diet was diverse, and although it was dominated by branchiopods and copepods, it included dinoflagellates and carideans and, interestingly, the adults and larvae of benthic species (in abundance). Numbers of the latter were greater by night than by day, although whether this reflected the vertical migration of predator (downwards) or prey (upwards) is unknown (Flynn & Gibbons 2007). The shallow nature of the lagoon (<8 m depth) may explain both the high numbers of benthos and the very low numbers of fish larvae recorded.

Indirect evidence of feeding comes from an examination of stable isotope ratios (^{13}C:^{12}C and ^{15}N:^{14}N) and fatty acids. Whilst not exactly revealing in details, a reanalysis of the data collected by van der Bank et al. (2011) from the edge of the inner shelf (~180 m) off Walvis Bay in 2008 shows that there are differences in the isotope signatures of both common species (Figure 11A, Supplementary Table 3). The $\delta^{15}N$ of *Chrysaora fulgida* (9.43 ‰ ± 0.92: $n = 48$) was significantly ($F = 20.40$. $p < 0.0001$) lower than that for *Aequorea forskalea* (10.72 ‰ ± 1.70: $n = 39$), as too was the $\delta^{13}C$ ($F = 10.96$. $p < 0.005$; −15.38‰ ± 1.05, −14.67‰ ± 0.92, respectively). These differences are supported by a multivariate analysis of fatty acids (Analysis of Similarity, ANOSIM global $R = 0.62$, $p = 0.001$) (Figure 11B), with the key differences between the two species shown in Supplementary Table 4. While *Chrysaora fulgida* and *Aequorea forskalea* are clearly different from the other dominant zooplankton in the area, they are also very obviously different from each other.

Parasitism

Hyperiid amphipods are well known as parasites/predators of a variety of gelatinous zooplankton, including salps, ctenophores and scyphozoans (Laval 1980). *Hyperia medusarum* is routinely collected from specimens of *Chrysaora fulgida* across the shelf off Namibia, and their distribution among hosts tends to display a negative binomial distribution. While amphipods are found in all tissues, there is a tendency for loads to be greater in the gonads (Buecher et al. 2001); they are also more common on animals with full stomachs (Flynn & Gibbons 2007). If we accept that the relatively low infestation rates observed by Buecher et al. (2001) reflect the loss of parasites following the trawl capture of jellyfish, there is a significant increase in infestation with increasing animal size (mass/diameter) (Brierley et al. 2004, Flynn & Gibbons 2007). However, evidence to suggest that increased parasite loads are associated with an altered body condition is contradictory (Flynn & Gibbons 2007 *cf* Brierley et al. 2004). Interestingly, parasite loads do not appear to materially impact on hydroacoustic backscatter, with the lion's share of the signal coming from the jellyfish and not the amphipods (Brierley et al. 2004).

Predation

Direct evidence of predation on jellyfish by other organisms in the Benguela is scant. That said, a hitherto undescribed species of *Drymonema* from the south-western Cape region of South Africa has been photographed eating *Pelagia* (Supplementary Figure 3A). Like other species of *Drymonema*, this animal is episodic in appearance and uncommon (Malej et al. 2014), so its impact on wider jellyfish populations is likely to be limited. In captivity, this species will readily feed on a variety of scyphozoans, including *Chrysaora fulgida* and specimens of *Aurelia*, but not the cubozoan *Carybdea murrayana* (Krish Lewis, Two Oceans Aquarium, Cape Town; personal communication).

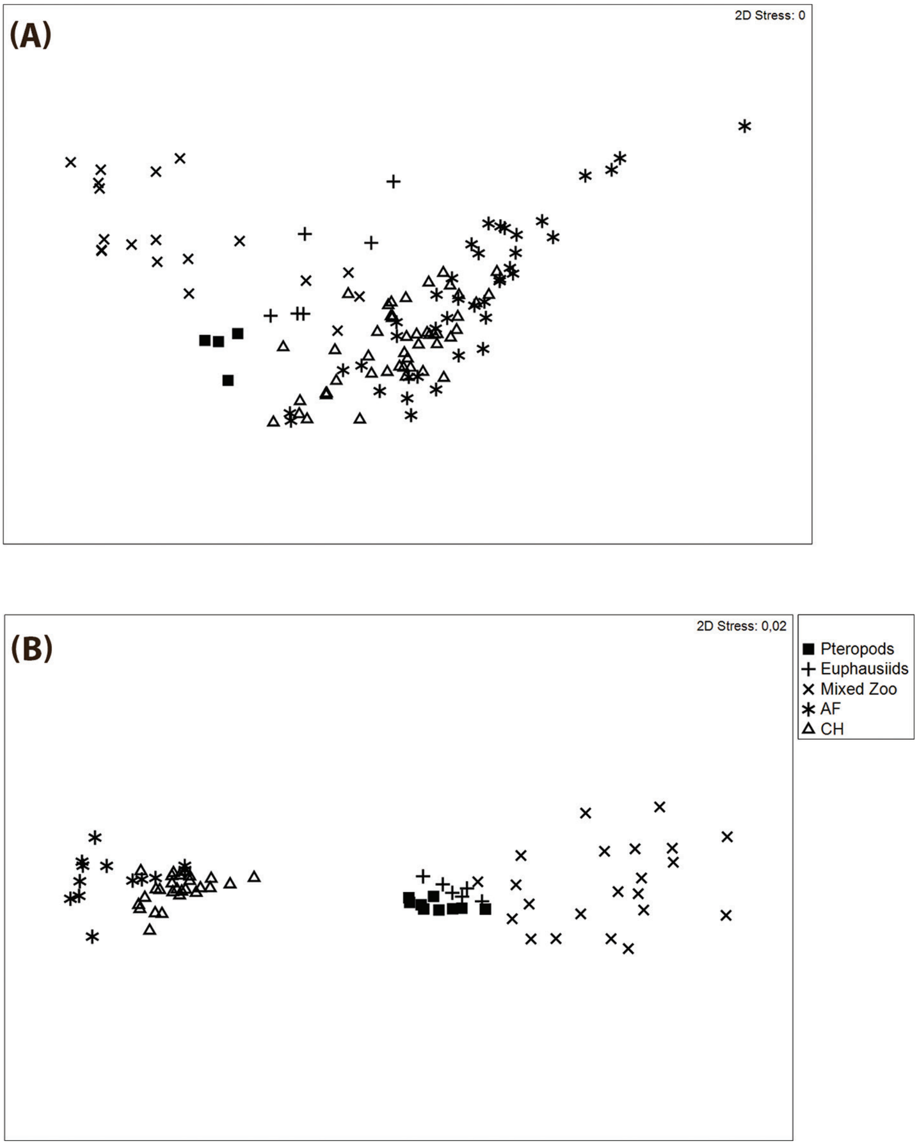

Figure 11 Non-metric MDS plots showing the similarity (Euclidean distance) in the stable isotope composition (^{13}C:^{12}C and^{15}N:^{14}N) (A) and fatty acid content (B) of planktonic organisms sampled off the coast of Namibia in April 2008. Isotope data were normalized, and fatty acid data were $\log_{10}(x + 1)$ transformed, prior to the construction of similarity matrices. All analyses computed using PRIMER7. Data extracted from van der Bank et al. (2011); fatty acid details shown in Supplementary Table 4.

The near-mutually exclusive, cross-shelf distribution of *Aequorea forskalea* and *Chrysaora fulgida* off Namibia has been remarked upon by several authors (Fearon et al. 1992, Buecher et al. 2001, Sparks et al. 2001). While the two species appear to favour slightly different environments (Sparks et al. 2001), the differences in distribution could reflect (in part) intraguild predation, because species of both genera are known to eat other gelatinous organisms (Feigenbaum & Kelly 1984, Purcell 1991). Species of *Chrysaora* are widely cultured in public aquaria, and growth to exhibition size is greatly improved by providing them with a diet that includes chunks of jellyfish of

Table 4 Seasonal changes in the percentage of catches of each of the dominant pelagic fish in the northern Benguela that also contained jellyfish (a); the percentage of total catch weight represented by catches that also contained jellyfish (b) and the ratio of catch weight with jellyfish vs. catch weight without jellyfish (c). Annual data also shown

Species		*Sardinops sagax*	*Engraulis encrasicolis*	*Trachurus capensis*	*Etrumeus whiteheadi*	*Sufflogobius bibarbatus*
Number trawls		**6045**	**1642**	**6330**	**2624**	**429**
a. Percent catches w jellyfish	Autumn	21	20	11	18	78
	Winter	37	52	38	54	65
	Spring	29	27	50	47	100
	Summer	15	20	10	17	60
	Annual	**26**	**33**	**12**	**24**	**70**
b. Percent biomass catches w jellyfish	Autumn	32	16	8	16	88
	Winter	38	59	32	42	90
	Spring	39	20	23	25	100
	Summer	15	2	10	26	58
	Annual	**34**	**44**	**9**	**25**	**69**
c. Catch wt w jellyfish / Catch wt wo jellyfish	Autumn	1.72	0.78	0.67	0.87	2.02
	Winter	1.59	0.66	0.29	0.38	n/a
	Spring	0.98	0.08	1.02	1.76	0.90
	Summer	1.06	1.34	0.76	0.62	4.55
	Annual	1.45	1.62	0.72	1.03	**0.97**

Source: Data collected over the period 1992–2006 and extracted from Utne-Palm et al. (2010).

another species (Widmer 2008a). *Chrysaora fulgida*, like the other species of *Chrysaora* found in some EBCs, has elaborately folded, voluminous oral arms basally (Supplementary Figure 1), which Bayha and Dawson (2010) have suggested might be an adaptation for medusivory. Interestingly, however, the stable isotope data published by van der Bank et al. (2011) show that *Aequorea forskalea* has higher values of δ^{15}N than *Chrysaora fulgida* in the waters offshore of Walvis Bay, although whether this reflects predation of the former on the latter or on a different resource base is unknown. Personal observations reveal that meta-ephyrae of *Chrysaora africana* readily consume ephyrae of *Chrysaora fulgida*.

What van der Bank et al.'s (2011) analysis does show, however, is that jellyfish represent a significant source of food for the bearded goby *Sufflogobius bibarbatus*, *Aequorea forskalea* being important for large gobies, whilst *Chrysaora fulgida* is similarly valuable for smaller fish. Although it is unknown whether the jellyfish eaten by the bearded goby are alive or dead at the time of consumption, the former is assumed (see below).

Beach-stranded jellyfish are quite quickly consumed by a variety of marine and terrestrial scavengers including whelks of the genus *Bullia,* as well as ghost crabs (*Ocypode cursor* Supplementary Figure 3B), whilst sea anemones will devour smaller species that drift too close to the seabed (Supplementary Figure 3C). Observations of beach-stranded jellyfish at Lüderitz have revealed a variety of coastal seabirds feeding on both *Chrysaora fulgida* and *Chirodropus gorilla*. Although the gonads of both these jellyfish species are the main target (Supplementary Figures 3D, E), smaller birds like sanderlings (*Calidris alba*) are attracted to the associated hyperiid amphipods (Supplementary Figure 3F).

Associations with fish

Approximately 70% of the pelagic catches (69% by biomass) of the bearded goby *Sufflogobius bibarbatus* made by the fishing industry off Namibia over the period 1990–2007 (*n* = 11324) also included jellyfish (Utne-Palm et al. 2010; Table 4). Either the bearded goby and jellyfish have a very similar distribution across the shelf, at the scale of the catch, or the bearded goby chooses to associate with jellyfish. Unlike most gobies, *Sufflogobius bibarbatus* has retained a swim bladder and displays DVM (Utne-Palm et al. 2010). It has been hypothesized that when bearded gobies move up into the water column at night in order to "re-oxygenate" their blood and digest their stomach contents (they have spent daylight in hypoxic bottom water, feeding and avoiding predators), they may deliberately associate with jellyfish (Utne-Palm et al. 2010). This strategy would serve to reduce predation pressure, as choice chamber experiments seem to suggest that bearded gobies are indifferent to the presence of jellyfish (*Chrysaora fulgida*), whilst some potential predators (*Trachurus capensis*) actively avoid them (Utne-Palm et al. 2010). At the same time that gobies use jellyfish as refugia, they may also be using them as a food source.

The data shown in Table 4 reveal that there is little in the way of microscale overlap in the distribution of *Trachurus capensis* and jellyfish. And less than 25% of small pelagic fish catches (anchovy, sardine and red-eye round herring) are also caught with jellyfish suggesting either a deliberate attempt at avoidance of jellyfish by skippers or a real difference in microscale pelagic habitat use. Unsurprisingly, there were no differences in the weight of goby catches with or without jellyfish, but interestingly, catches of sardine and anchovy were almost 50% bigger when they co-occurred with jellyfish (Table 4). This level of overlap between jellyfish and small pelagic fishes is one of the main reasons why applications to fish for jellyfish off Namibia have been rejected: the risk of a significant sardine or anchovy by-catch is incompatible with efforts to regrow pelagic fish stocks.

A spatial and dietary overlap between jellyfish and small pelagic fishes in other EBC systems (see below) has led to concerns that competition between the two groups may occur. The isotopic comparisons generated by van der Bank et al. (2011) suggest that *Aequorea forskalea* feed at the same trophic level as anchovy and small horse mackerel ($\delta^{15}N \approx 12‰$; Iitembu et al. 2012), whilst *Chrysaora fulgida* feed at the same trophic level as sardine ($\delta^{15}N \approx 9‰$; Iitembu et al. 2012). Anchovy and small horse mackerel feed predominantly on meso- and macro-zooplankton (James & Findlay 1989, Kadila et al. 2020), whilst sardine will switch between phytoplankton and mesozooplankton, depending on ambient prey densities (van der Lingen 1994, van der Lingen et al. 2006).

Using historical fisheries and survey data (1991–2011), Tjizoo (unpublished) noted a spatial separation of *Chrysaora fulgida* and horse mackerel off Namibia: the former occurring mostly in cool water (<15°C) off central Namibia, while the latter were more common in warmer waters further north. Data seem to suggest that horse mackerel are more broadly distributed over the shelf relative to *Chrysaora fulgida*, which is confined to waters less than 100 m bottom depth. As adult horse mackerel adopt to mesopelagic and demersal zones with maturity (Barange et al. 2005), *Chrysaora fulgida* only overlap spatially with juvenile horse mackerel that inhabit coastal epipelagic zones. Isotopic data indicate pronounced trophic overlaps between *Chrysaora fulgida* and juvenile horse mackerel, as they feed at the same trophic level (2.5). It has been suggested that this difference in environmental preference allows the spatial co-existence of horse mackerel and *Chrysaora fulgida* in the northern Benguela ecosystem.

Fisheries and human activities

Estimates of pelagic fish biomass in South Africa and Namibia are usually derived from multi-frequency hydroacoustic surveys. Despite the fact that acoustic target strength estimates have been determined for *Chrysaora fulgida* and *Aequorea forskalea* (Brierley et al. 2001, 2004, 2005) and that algorithms have been developed to discriminate between jellyfish and pelagic fishes, these tools are not regularly employed by fisheries management authorities.

Research trawls off central Namibia regularly capture *Chrysaora fulgida* in such quantities that repairs to nets are required. And this after trawls of short duration. And "as noted by Venter (1988), the high biomass of jellyfishes in the late 1970s had become a nuisance to fishermen and interfered with fishing operations in the region by clogging and damaging nets" (Roux et al. 2013, pp. 253).

Whilst jellyfish have yet to cause any blockages of the intake pipe for the desalination plant just north of Swakopmund in Namibia, *Chrysaora fulgida* has forced the temporary closure of the nuclear power plant at Koeberg, just north of Cape Town in South Africa. The plant, which is operated by ESKOM, is the only nuclear power station on the African continent and first became operational in mid-1984. At full capacity, the plant can deliver 1940 MW to the national grid, its two pressurized water reactors requiring 80 m^3 seawater s^{-1} to do so. Although the plant is provided with a specially constructed intake basin, this became inundated by extensive jellyfish blooms in May 2005 and March 2020, which blocked the drum filters causing temporary shutdowns to power generation.

Macromedusae in ecosystem models

A number of foodweb models have been constructed in the Benguela region since the late 1990s, generally distinguishing the southern Benguela off South Africa and the northern Benguela off Namibia and southern Angola due to the perception that many commercial fish stocks were distinct between the two sub-regions and because of different fisheries management history and regimes. With the exception of the models presented in Heymans et al. (2004) which combined jellyfish in a single "zooplankton" group, the other models contained an aggregated "*gelatinous zooplankton*" functional group. However, the parameterization of the models around the jellyfish functional group was made through untested assumptions due to a complete lack of data or estimates on the most important parameters concerning this group (biomass, growth, diet, consumption rates, predation, survival, etc.). It should also be noted that some of these early models (Heymans 1996, Heymans and Baird 2000a,b) erroneously assumed a jellyfish diet dominated (84.1%) by phytoplankton, which resulted in a misrepresentation of this functional group in the foodweb. It is now accepted that most of the biomass of gelatinous zooplankton in the region is composed of *Aequorea forskalea*, *Chrysaora fulgida* and other planktivorous carnivores.

The next series of foodweb models were also designed using the ECOPATH approach (Christensen & Pauly 1992) and were constructed similarly for the southern and northern Benguela. These models were aimed at highlighting gaps in knowledge about some potentially important functional groups and describing the trophic flows around the main commercially exploited fish stocks. The overall intention was to use these models to open the way for a possible multispecies approach of fisheries management in the Benguela region (Jarre-Teichmann et al. 1998, Shannon & Jarre-Teichmann 1999). In the absence of empirical data on jellyfish in either sub-systems, those models assumed a jellyfish biomass of one million t in the southern Benguela and five million t in the northern Benguela. These assumptions of wet mass were then converted to carbon (assuming 98%–99% water content and a conversion factor of 0.4 for dry mass to carbon). The diet was partitioned equally between phytoplankton, detritus (bacteria), micro- and mesozooplankton (25% each). Production over biomass (for tissue) was assumed to be half that of the estimate for macro-zooplankton, while other parameters were assumed to be similar to that of macro-zooplankton. With very little information on predators of jellyfish in the Benguela region, the inevitable conclusion of these modelling exercises showed that jellyfish seem to have a relatively unimportant role, with a very low "ecotrophic efficiency", in the trophic flows of those two sub-systems. However, the potential competitive interactions with small pelagic fishes (sardine and anchovy in particular) were highlighted in both studies, as well as caution regarding the interpretation of these preliminary results, due to the very high level of uncertainty surrounding the assumed parameters concerning the jellyfish functional group.

By using both ECOPATH models built for different time periods and dynamic simulations within the models (ECOSIM, Walter et al. 1997), as well as more up-to-date information about jellyfish, we have highlighted some possible important changes in the northern Benguela foodweb since 1970 (e.g. Roux & Shannon 2004, Watermeyer et al. 2008). In comparison with other EBC systems, the structure of the present northern Benguela ecosystem is exceptional, being characterized by a very low biomass of small pelagic fish and a very high biomass of jellyfish (Moloney et al. 2005, Shannon et al. 2009). These studies have emphasized an increase in pelagic-benthic coupling in the northern Benguela, by comparing both with other EBC systems and that of the northern Benguela prior to the sardine collapse. The structural change that accompanied the collapse of small pelagic fish collapse and the increase in jellyfish biomass was a probable redirection of flows away from predators in the pelagos (marine mammals, seabirds and predatory fish) to the benthos and detritus. This led to a drop in the efficiency of the major trophic pathways supporting the dominant commercial fisheries. These possible changes in the trophic structure of the northern Benguela have been supported by most time series of trophodynamic indicators (e.g. Cury et al. 2005). It must be noted that the linkages between jellyfish and other functional groups in these models were still not well understood, and there was a wide uncertainty in the parameterization and dynamics of the models with regard to jellyfish (Roux & Shannon 2004, Shannon et al. 2009).

A more recent study by Roux et al. (2013) supports the hypothesis that the overfishing of sardine resulted in the collapse of the stock in the northern Benguela, which triggered an increase in jellyfish in this system. This comparative study of the southern and northern Benguela combined commercial fisheries data, trophodynamic indicators, predator diet and energetic information, as well as foodweb modelling outputs over more than four decades (Roux et al. 2013). The resulting changes in the foodweb structure were found to be profound and indicated a possible alteration to the wasp-waist trophic control structure of the ecosystem. In the latter, abundant populations of small pelagic fishes as the main and efficient energy conduit from producers to higher trophic levels and exert a top-down trophic control on producers (plankton) and a bottom-up trophic control over higher trophic levels (e.g. Cury et al. 2000, Shannon et al. 2000, Cury & Shannon 2004). The altered state of the northern Benguela ecosystem, which includes a dominance of jellyfish in biomass on the other hand, seems to be characterized by an increased pelagic-benthic coupling, an increased flow to detritus and a reduced efficiency of energy transfer towards higher trophic levels.

Based on our present understanding of the regional ecosystem, jellyfish could have been a major contributing factor in the dramatic changes observed in the northern Benguela, together with the sardine stock (e.g. Roux et al. 2013). However, there are many gaps in the basic data that prevent us from fully understanding the trophic interactions that led to these changes. Priority should be given to refining both biomass estimates (and investigating possible seasonal variability) and the basic parameters to be used in foodweb models (diet composition, growth parameters, consumption and assimilation rates, predation, survival, etc.). Incorporation of these missing data in foodweb models should allow a better understanding of the role of jellyfish in the foodweb and the past and present changes in their dynamics. The likely results are expected to be essential for an improvement in the scientific advice aimed at an application of an ecosystem approach to fisheries management in the region.

The Humboldt ecosystem

Description

The Humboldt Current System is the most productive eastern boundary upwelling system in terms of fish productivity and is one of the most productive ecosystems in the world ocean; it supports one of the largest single-species fisheries (Peruvian anchovy *Engraulis ringens*) (Chavez et al. 1999, 2008, Pennington et al. 2006). The system is the equatorward flowing, eastern portion of the basin-scale southeast Pacific anticyclonic gyre. The Humboldt Current system extends from southern Ecuador and the Galapagos Islands (~1°S), where cold upwelled waters are limited by warm tropical waters of the equatorial front, to southern Chile (~42°S) where water masses are bounded by the West Wind Drift (Thiel et al. 2007). The Humboldt Current system is bounded by the meridionally oriented coastline of South America and a narrow continental shelf (Figure 12).

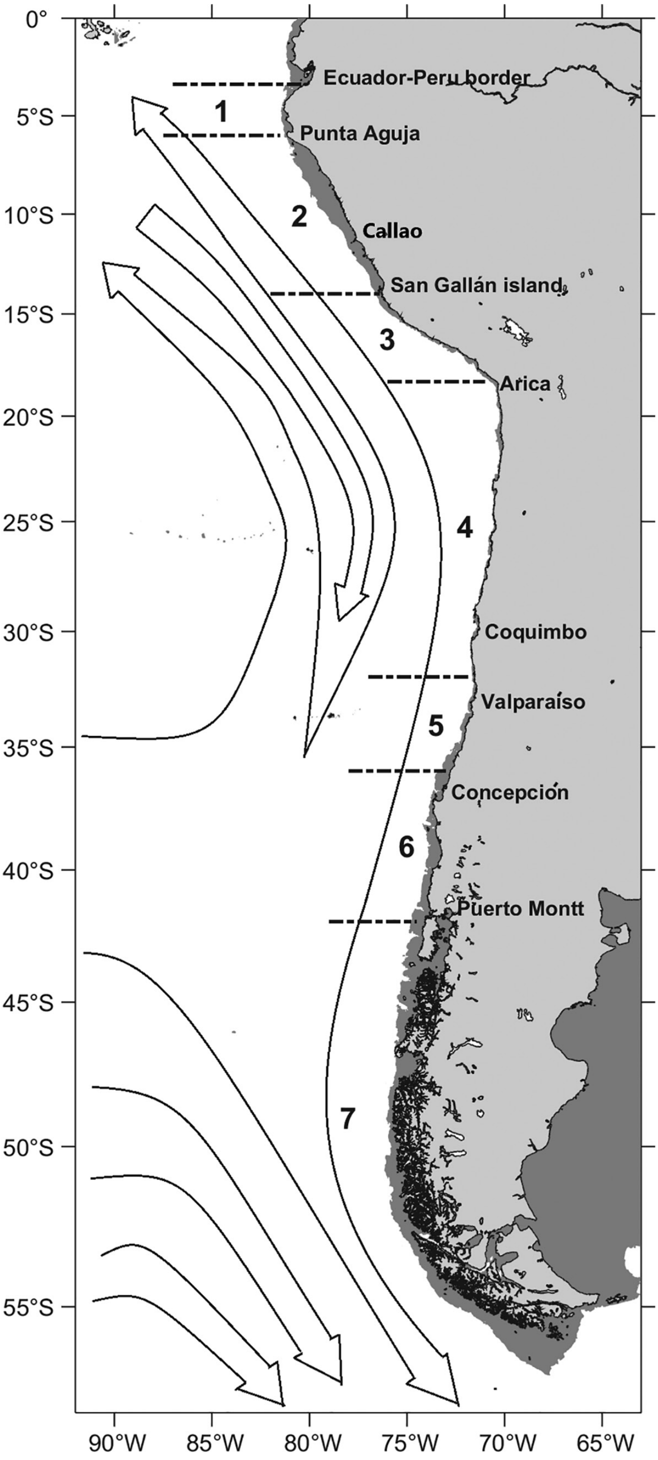

Figure 12 Outline map of western South America showing the approximate positions of the major coastal currents in the Humboldt system: the continental shelf is shaded. The numbers (1–7) refer to distinct latitudinal regions that are discussed in the text.

The width of the Peruvian continental shelf is variable and is in direct relation to the geodynamics of the shelf break: it can be divided into three latitudinal areas (Figure 12). In the north (area 1 in Figure 12), from the Ecuador–Peru border (3°23′S) to Punta Aguja (6°S), the continental shelf is relatively narrow and the shelf break is parallel to the coastline. The shelf-width varies between 6 and 60 km offshore until Máncora (4°05′S), and almost disappears between Cabo Blanco (4°15′S) and Punta Pariñas (4°40′S) before widening again (25–35 km) to Sechura Bay (5°45′S). In the central region (area 2 in Figure 12), between Punta Aguja and San Gallán Island (14°S), the shelf is relatively wide between Pimentel (6°50′S) and Chimbote (9°03′S) (100–130 km offshore), and then, it narrows towards the south between Huarmey (10°S) and Callao (12°S) (55–75 km offshore). In the south (area 3 in Figure 12), between San Gallán and the Peruvian–Chilean border (18°20′S), the shelf break is particularly narrow and can be found between 10 and 25 km offshore (Schweigger 1964, Teves & Evangelista 1974, Morales et al. 2020).

The Chilean coast can be divided into four latitudinal regions. North of ~32°S (area 4 in Figure 12) the shelf is extremely narrow (<10 km offshore) and receives little freshwater influence; between 32 and 36°S (area 5 in Figure 12), there is a widening shelf with low and scattered river inflow; and from 36 to 42°S (area 6 in Figure 12), the shelf is wider (~70 km offshore) and is seasonally influenced by freshwater inflow, and the southern region (>42°S; area 7 in Figure 12), which has a wider topographically complex, fjord-indented coastline and experiences strong river runoff (Figueroa 2002, Riascos et al. 2009). Offshore, the continental shelf, the deep canyons associated with river basins and the Atacama Trench off the Peruvian–Chilean coast play an important role in biogeochemical cycles, which may be highly sensitive to climatic change (Thiel et al. 2007, Aguilera et al. 2019).

Three key features distinguish the physical and chemical conditions of the Humboldt Current system among EBC systems. First, it extends closer to the equatorial line than any other major EBC system. Second, there is an intense and extremely shallow oxygen minimum zone (OMZ) – a thick layer of water whose upper limit is located at a few tens of metres below the surface, and where oxygen concentrations are so low that, except for bacteria, few species can adapt or temporarily survive (Chavez et al. 2008, Bertrand et al. 2018). Third, the Humboldt Current system is the region where the effects of El Niño and La Niña phases of El Niño-Southern Oscillation (ENSO) are most notable (Chavez et al. 2008). These last two features are expected to change in a warming climate. Model projections and observational data suggest a deoxygenation trend and an intensification of coastal upwelling-favourable winds in poleward portions in EBCs under future climate scenarios (e.g. Levin 2018). In turn, climate projections show that extreme El Niño and La Niña episodes are likely to occur more frequently with unabated greenhouse gas emissions (Cai et al. 2015, Wang et al. 2019). Evidence is emerging that changes in ENSO behaviour have occurred, with El Niño episodes differing substantially in their spatial pattern, intensity and impact. Canonical Eastern Pacific episodes display strongest surface thermal anomalies in the far eastern equatorial Pacific, whereas peak ocean warming occurs further west during Central Pacific episodes sometimes referred to as “El Niño Modoki”. The latter type has become more common in recent decades relative to past centuries, a trend that is projected by some studies to continue with ongoing greenhouse warming (Freund et al. 2019). Furthermore, climatic regimes and marine ecosystem functioning in the Humboldt Current system are being modified by a wider array of ocean and land-based human activities, including pollution, resource harvesting, increased nutrient input, habitat destruction and ocean sprawling (Gutiérrez et al. 2016, Halpern et al. 2008, Riascos et al. 2019).

The South Pacific High represents the main forcing for equatorward upwelling-favourable winds in the Humboldt Current system, which display considerable spatial and temporal variability. The following is a brief description of this variability, which has been analysed in detail by Thiel et al. (2007). North of ~35°S winds remain upwelling-favourable throughout the year up to ~5°S, where the seasonal north–south migration of the Inter-Tropical Convergence Zone brings winds and precipitation, thus favouring the stratification. Three provinces of maximum alongshore wind stress can be identified in this zone (Thiel et al. 2007, Gutiérrez et al. 2016). The most productive province is located off Peru, where strong offshore Ekman transport creates a coastal productive belt that ranges between 100 and 200 km with an average annual primary production rate of 1.2 $kg{\cdot}C{\cdot}m^{-2}{\cdot}yr^{-1}$. In Peru, this high primary productivity supports a fishery at least 20 times greater in landings than other similar upwelling boundary current ecosystems worldwide (Bakun & Weeks 2008). Off central Chile (centred at ~30°S), the mean annual primary production rate is over 1 $kg{\cdot}C{\cdot}m^{-2}{\cdot}yr^{-1}$, with a strong seasonal fluctuation. The northern Chilean coast is a narrow (<50 km) productive province, with annual primary production rate of 0.66 $kg{\cdot}C{\cdot}m^{-2}{\cdot}yr^{-1}$ and low seasonality. South of ~35°S, seasonality in the influence of the South Pacific High promotes an alternation between summer upwelling maximums and winter conditions characterized by poleward, downwelling-favourable winds driven by storms associated with the polar front (Shaffer et al. 1999, Rutllant et al. 2004). Moreover, coastal stratification imposed by freshwater runoff becomes important even during summer upwelling conditions (Atkinson et al. 2002).

Off Peru, primary production during winter is negatively correlated with upwelling favourable winds intensity, which seems explained by the light limitation imposed by deeper wind mixing, while in summer, the decreased upwelling strength allows periods of thermal stratification that foster phytoplankton blooms (Gutiérrez et al. 2016). Periods of decreased upwelling strength – associated with warmer SST – off Peru are concomitant with decreases in the larger size fraction of phytoplankton (i.e. chain-forming diatoms) at seasonal and interannual scales (Ochoa et al. 2010). Off northern Chile, the highest primary production is associated with microphytoplankton mostly restricted to a narrow inshore zone, whereas pico- and nanophytoplankton predominate offshore, with little seasonal fluctuations. Off central Chile, primary production is associated with upwelling-favourable winds, which predominate during the spring and summer months. Phytoplankton assemblages proliferating off the Chilean coasts are mostly dominated by no more than 10 species of chain-forming diatoms (Thiel et al. 2007).

In terms of biomass, the zooplankton community in the Humboldt Current system is dominated by large copepods and euphausiids (Thiel et al. 2007, Ayón et al. 2008, Aronés et al. 2019). Off Peru, the continental shelf is dominated by *Acartia tonsa* and *Centropages brachiatus*, but species composition and biomass vary on short time scales due to advection and interspecific interactions. Upwelling intensity drives seasonal variability of zooplankton biomass and composition, while ENSO represent a major driving force for community changes at interannual scales (Ayón et al. 2008). Off the Chilean coast, the zooplankton community is dominated by two species endemic to the Humboldt Current system (*Calanus chilensis* and *Euphausia mucronata*), several cosmopolitan species and a typical tropical species (*Eucalanus inermis*) (Marín et al. 1994, Hidalgo & Escribano 2001). The OMZ interacts with zooplankton that typically aggregate near upwelling centres (Escribano & Hidalgo 2000); epipelagic species concentrate in surface waters without exhibiting DVMs, but some euphausiids may temporarily enter this zone, and some copepods may even inhabit this zone (Antezana 2002, Escribano 1998, Hidalgo et al. 2005)

Industrial fisheries in the northern Humboldt Current system developed in the mid-twentieth century, and there is some indication that the recent time period represents a period of exceptional productivity in relation to that of the last thousand years (Chavez et al. 2008, Gutiérrez et al. 2009, Salvatteci et al. 2018). The main landed species are the Peruvian anchovy, the Chilean jack mackerel (*Trachurus murphyi*), the jumbo flying squid (*Dosidicus gigas*), the common sardine (*Strangomera bentincki*), the Pacific chub mackerel (*Scomber japonicus*) and the Pacific sardine (*Sardinops sagax*) (Gutiérrez et al. 2016). At present, the Peruvian anchovy represent the main pelagic fish resource in the Humboldt Current system (84% and 34% of fish landings composition off Peru and Chile, respectively) in comparison with the Pacific sardine (26% of fish landings in Chile) for the period 2009–2013 (Gutiérrez et al. 2016). A regime shift has long been proposed between an anchovy-dominated state and a sardine-dominated state in the Humboldt Current system, related to long-term ENSO-related variations in oceanographic conditions and mediated by the availability of prey items (Alheit & Niquen 2004, Espinoza & Bertrand 2008, Ayón et al. 2008). A reconstruction of the ENSO in the Holocene (10,000 years) showed that ENSO variance was close to the modern level in the early Holocene and severely damped ~4000–5000 years ago. The modern ENSO regime was established ~3000–4500 years ago, being sensitive to changes in climate boundary conditions during the whole Holocene (Carré et al. 2014). Recent studies based on fish scale remains suggest that shifts are related to upwelling-dependent habitat changes driven by regional and large-scale forcing (Salvatteci et al. 2018). However, climate change may shift the system out of its current productive state; global models predict a moderate decline in catch potential between 2050 and the end of the century (Cheung et al. 2018).

Owing to competitive trophic interactions between jellyfish and forage pelagic fish and projected physical changes under expected greenhouse-associated warming in the Humboldt Current system, Bakun et al. (2010) predicted that overexploitation of small pelagic fishes would define the balance between a fish-dominated state and a much less desirable jellyfish state. As some of the most important fish resources in the system are either collapsed, overexploited, fully exploited or unmanaged (Gutiérrez et al. 2016), we are left with the message that there is much to learn yet about jellyfish in the Humboldt Current system.

Macromedusae

Species composition

The last census of cnidarians carried out around the coasts of Latin America (Oliveira et al. 2016) shows that the most important macromedusae recorded in the Humboldt Current system are the scyphozoans *Chrysaora plocamia*, *Pelagia noctiluca* (Family Pelagiidae), *Phacellophora camtschatica* (Family Phacellophoridae), *Aurelia* sp. (Family Ulmaridae), *Stomolophus meleagris* (Family Stomolophidae) and an unidentified Lobonematidae, as well as the large Hydromedusae *Aequorea coerulescens*, *Aequorea forskalea*, *Aequorea globosa* and *Aequorea macrodactyla* (Family Aequoreidae). In addition, some deep-water species have been recorded including *Atolla chuni*, *Atolla wyvillei* (Family Atollidae) and *Periphylla periphylla* (Family Periphyllidae).

In the Humboldt Current system, the most common and abundant species, particularly during spring and summer, is *Chrysaora plocamia* (Supplementary Figure 4). This species is abundant between Punta Falsa (6°S) in northern Peru to Antofagasta (23°40′S) in northern Chile, a distance exceeding 2400 km (Mianzan et al. 2014, Quiñones et al. 2018). It is less commonly found southwards along the Patagonian shelf to the southern tip of Chile (55°S). On the Atlantic Ocean coast, this species is also present in northern Patagonia (Mianzan et al. 2014).

Unpublished reports and by-catch information from IMARPE indicate that *Pelagia noctiluca* is mainly distributed in the offshore waters off Peru, although it may occur at the Peruvian coast in low numbers and even occasionally in the coastal waters of northern Chile. *Phacellophora camtschatica* has been recorded only along the northern coast of Peru between Paita (5°S) and Punta Guañape (8°27′S) and mainly in oceanic waters (IMARPE, unpublished data). In Chile, this species has been collected from near-surface, neritic waters between 18 and 43°S (Fagetti 1973, Kramp 1952, 1968). Moon jellyfish *Aurelia* sp. have been recorded off Sechura Bay in Peru (5°19′S, 81°16′W: L. Caccha personal communication), and in southern Chile from 53°S to ~55°S in the Patagonian interior waters (Häussermann et al. 2009, Pagès & Orejas 1999, Palma et al. 2014). The rhizostome jellyfishes *Stomolophus meleagris* and *Versuriga* sp. have been reported from stranding events in northern Peru (between ~3 and 9°S), but neither has been documented as occurring off Chile.

Several species of the large hydrozoan genus *Aequorea* have been recorded in the Humboldt Current system. These species occur in relatively low numbers in coastal and offshore waters. Medusae of *Aequorea coerulescens* have been registered from 3°30′ to 43°S (Fagetti 1973, Kramp 1966, 1968, Palma et al. 2011), *Aequorea forskalea* occurs from 37 to 52°S (Kramp 1957), *Aequorea globosa* is found south of Concepción Bay (Chile) at 38°8′S (Fagetti 1973, Kramp 1966) and from

41°30′S to 43°38′S along the Chiloé Interior Sea (Palma et al. 2011), and *Aequorea macrodactyla* has been reported from 18°30′S to 55°50′S (Fagetti 1973, Kramp 1965, 1968, Pagès & Orejas 1999).

Distribution

Space There is limited information from incidental catches from the scientific cruises carried out by IMARPE to survey fisheries resources. These surveys indicate that *Pelagia noctiluca* is more abundant in waters offshore of the shelf break between Punta Sal (4°S) to Islay (17°S), and big blooms have been registered between 7 and 12°S, where they are associated with the presence of Subtropical Superficial Water (SSW). This species has been noted in neritic waters and although it usually occurs in low numbers, a big bloom was observed during autumn 2016 some 10 km offshore of Puerto Morin (~8°30′S), which was coincident with a Modoki – El Niño event with sea surface anomalies of 2.2–2.7°C above the historic record (NOAA 2020) and with a strong eastward intrusion of SSW.

Most of the information about the distribution of macromedusae in the region applies to *Chrysaora plocamia*. Throughout its range in the Humboldt Current system, *Chrysaora plocamia* is patchily distributed (Oliveira et al. 2016, Palma et al. 2014), although abundances are much higher off Peru than off southern Chile (Mianzan et al. 2014). It is difficult to disentangle the effect of time on distribution as distribution (and abundance) varies considerably between climatic periods (e.g. El Niño vs. La Niña scenarios), which reflects the species' response to changes in the environment (Quiñones et al. 2018).

During El Niño years, both the spatial distribution and abundance of *Chrysaora plocamia* are expected to increase (Quiñones et al. 2015). Such years are accompanied by very weak winds, which produce little mixing and lead to a highly stratified water column with a deep thermocline. Cold, nutrient-rich bottom waters do not outcrop at the surface and phytoplankton communities are dominated by small and motile cells that in turn favour small zooplankton: a seemingly perfect environment for *Chrysaora plocamia* (Figure 13A). Massive blooms of this species have been observed in pelagic waters of the northern Humboldt Current system between 6 and 18°S and within 75 km of the coast (extending to 280 km offshore) during the early stages of strong El Niño years such as 1982/1983 and 1986/1987 (Quiñones et al. 2018) (Figure 14). When El Niño SST anomalies become stronger, there is a southward migration to between 14 and 18°S, and it is assumed that this southward migration could reach to Antofagasta (~23°S).

During neutral (or slightly warm) years, *Chrysaora plocamia* occurs at high abundances only in neritic waters (Figure 13B). Such was observed in 2014, when *Chrysaora plocamia* was restricted to the nearshore zone within 35 km from the coast and mainly between 6 and 14°S. Neutral years are characterized by a local relaxation of upwelling, which leads to reduced mixing and waters with a low concentration of nutrients; phytoplankton communities are dominated by flagellates and dinoflagellates. Although the effects of these altered environmental conditions on the growth and survival of *Chrysaora plocamia* are unknown (Figure 13B) (Quiñones 2018), they are clearly not favourable to large extensive populations.

During La Niña years, *Chrysaora plocamia* appears to be absent in pelagic coastal and offshore waters (Figure 13C), but persists below the thermocline in the subsurface waters of semi-enclosed areas. Such was observed in 2007 and 2013. The environment is characterized by strong coastal winds, leading to high levels of turbulence and a well-mixed water column rich in nutrients that leads to abundant large phytoplankton but few micro-gelatinous organisms and small zooplankton, which limits the growth and survival of *Chrysaora plocamia* and relegates them to subsurface shallow and semi-protected areas like Independencia Bay (14°14′S).

Space-time Medusae of *Chrysaora plocamia* are present in the water column of the Humboldt Current system for between 9 and 10 months of the year, from mid-winter until late autumn or early winter. Off southern Chile not a single individual was captured during winter surveys of 2006 (Palma et al. 2011) or 2007 (Bravo et al. 2011). Off southern Argentina (42–46°S), post-ephyra and

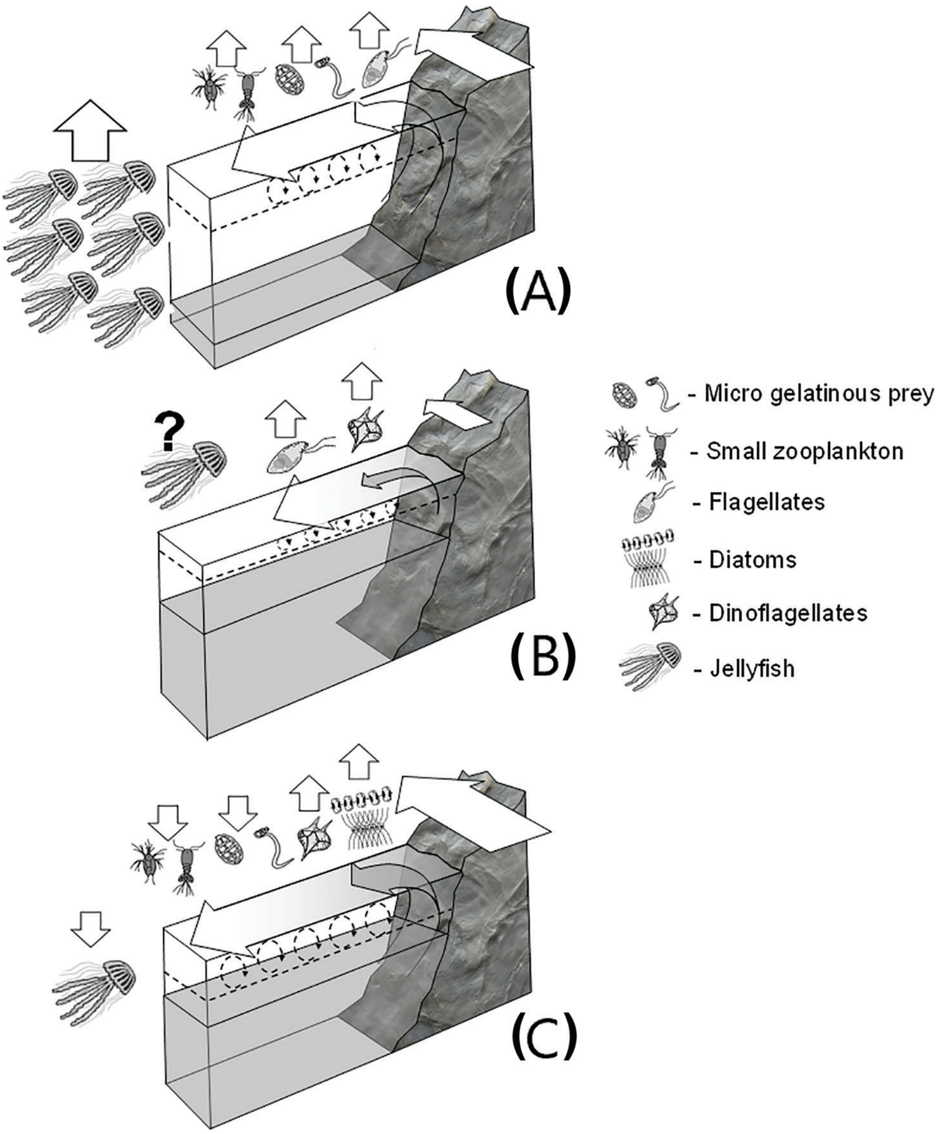

Figure 13 Diagram of the variability in the productivity of the northern Humboldt Current system at inter- and intra-annual level. The thermocline is represented by the separation between the light and the shaded layer; the shaded layer represents cold, nutrient-rich waters below the thermocline. The coastal wind strength is represented by the width and size of the white arrow parallel to the coast. The mix layer in the water column is represented by the cut line and eddies. The Ekman degree of transport is represented by the white line perpendicular to the coast. (A) Typical “El Niño” year with high productivity of *Chrysaora plocamia*, (B) neutral period with uncertain productivity of *Chrysaora plocamia*, (C) typical cold year or “La Niña” with low production of *Chrysaora plocamia* (adapted from Ochoa et al. 2010).

juveniles have been observed in spring (Mianzan 1989), sexually mature individuals were found between summer and autumn, and a few senescent, damaged and decomposing individuals have been noted in late autumn (Mianzan et al. 2014, Schiariti et al. 2018).

Data suggest that moving southwards through the Humboldt Current EBC system, *Chrysaora plocamia* becomes more temporally restricted in appearance. Sighting surveys conducted in

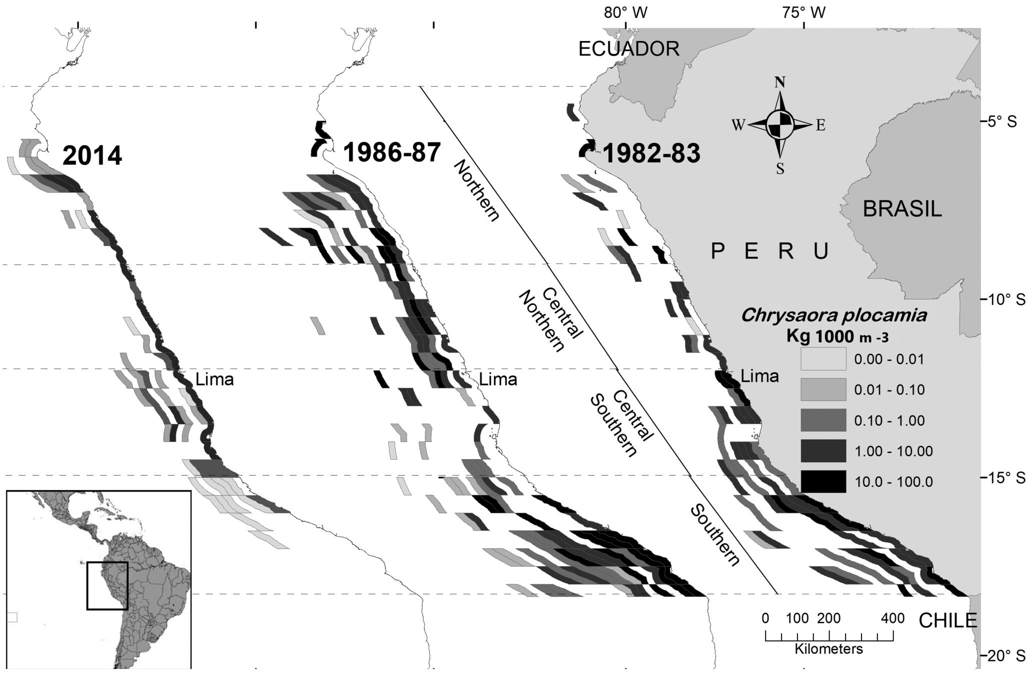

Figure 14 Spatial biomass distribution of *Chrysaora plocamia* by iso-paralitoral areas during El Niño years (1982–1983, 1986–1987) and during a neutral year (2014). Abundance is expressed in kg 1000 m^{-3}.

Independencia Bay (14°14′S) suggest that *Chrysaora plocamia* is most abundant and animals are most conspicuous (largest) during summer and autumn (Table 5A, Figure 15), and this agrees with the results of by-catch surveys in the artisanal purse seine fishery in the same area (Table 5B). Off Mejillones Bay (~23°S) in northern Chile (Figure 16), *Chrysaora plocamia* is mainly found between November and January (summer), while in central Chile, sightings of *Chrysaora plocamia* are restricted to summer; off southern Chile its appearance is transient, with densities of up to 93 individuals 1000 m^{-3} during spring (Palma et al. 2011). Mass die-offs of *Chrysaora plocamia* have been observed in Peru during early winter on two occasions: in Bahia Independencia (14°20′S) in 2012 and in Puerto Eten (06°30′S) in 2018 (Quiñones unpublished data). During these events, dead and dying specimens accumulated at the seafloor and this suggests that the majority of the population dies after sexual reproduction, mainly during autumn or early winter (Decker et al. 2014). It is important to note that adult *Chrysaora plocamia* have been recorded in the middle of winter, but only on two occasions (2012 and 2018), implying that overwintering in Peru is an unusual occurrence.

As noted above, the abundance of *Chrysaora plocamia* is strongly influenced by the state of the climate. The results of an IMARPE study conducted over a 42-year period from 1972 to 2014

Table 5A Seasonal changes in the number of sightings of *Chrysaora plocamia* the water column in Independencia Bay, during 2004–2007

Season	Number of stations with jellyfish	Total number of sighted jellyfish	Jellyfish area (km^2)
Spring	48	474	3.82
Summer	127	1045	22.43
Autumn	73	610	10.29
Winter	3	7	0.07

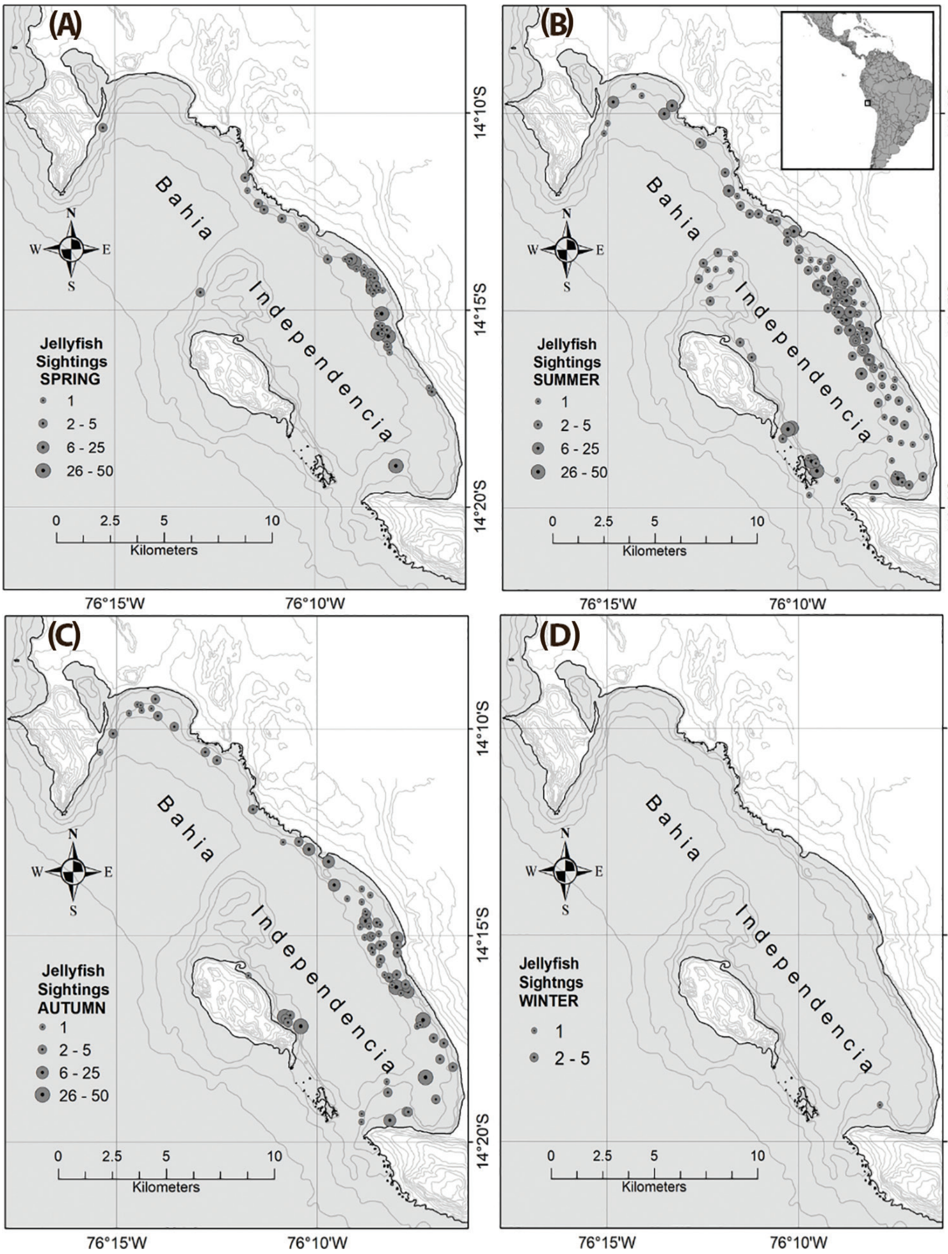

Figure 15 Seasonal changes in the abundance of *Chrysaora plocamia* in Independencia Bay, central Peru (pooled data for 2004–2007). Open circles represent scuba diving sightings in the water column, and size of the circle means abundance per sighting (Quiñones unpublished).

indicate that between 1972 and 1989, abundances were highly variable, ranging from (averages of) zero to 12 kg 1000 m^{-3}. A dramatic decrease was noted early in the second period (1989), and jellyfish were extremely rare or absent for the next 20 years. However, a small increase is recorded at the end of the time series (2009–2014: see Figure 2 in Quiñones et al. 2015). The pattern of two distinct periods coincides with warm–cold interdecadal fluctuations known as the El Viejo and La Vieja regimes (Chavez et al. 2003), respectively. Both regimes are visualized in the Regimen Indicator

Table 5B Jellyfish (*Chrysaora plocamia*) by-catch (kg jellyfish 1000 m^{-3} of filtered seawater) in the artisanal purse seine fishery of Pisco (Oct 2016–Sep 2017)

Season	Mean captures	Standard error	Total numbers of hauls
Spring	0.00498	0.0028	798
Summer	0.05378	0.0129	643
Autumn	0.00291	0.0014	950
Winter	0.00021	0.0001	991

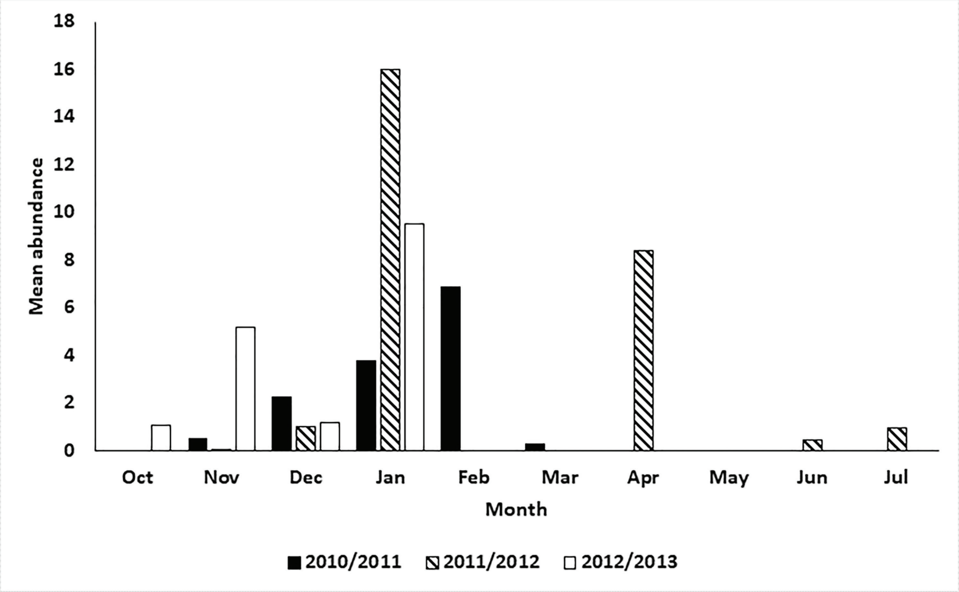

Figure 16 Monthly changes in the abundance (individuals per sighting) of *Chrysaora plocamia* in Mejillones bay between 2010 and 2013. Estimations are based on between 45 and 55 sightings performed by scuba divers in surface waters (max 15 m water depth) (Riascos unpublished).

Series (RIS3) (Kamikowski 2012), which shows a positive regime between the early and mid-1970s to the early 1990s, and then a negative regime between the 1990s and 2000s. This same pattern is evidenced in anchovy catches and fishing effort, with reduced landings noted during the El Viejo warm regime (positive RIS3 values) and increased landings during the La Vieja regime (negative RIS3 values; Quiñones et al. 2015).

In the northern Humboldt Current system, medusae tend to be small during spring, and then grow and mature through the following seasons to attain maximum size in autumn (Figure 17). It is assumed that a single seasonal cohort is produced around mid-winter, although additional cohorts may be generated during spring. No small individuals have ever been seen during summer or autumn, implying that strobilation only occurs during late winter and spring (Quiñones unpublished data). Considering that Figure 17 represents seasonal changes in body sizes over several years' worth of measurements, it must be assumed that most of the adult population consistently dies by the end of autumn. Off Mejillones Bay in northern Chile, by contrast, there is a suggestion that some large, sexually mature medusae may appear during October–November (Figure 18), and these likely represent overwintering adults from the previous year (Ceh et al. 2015). Thereafter,

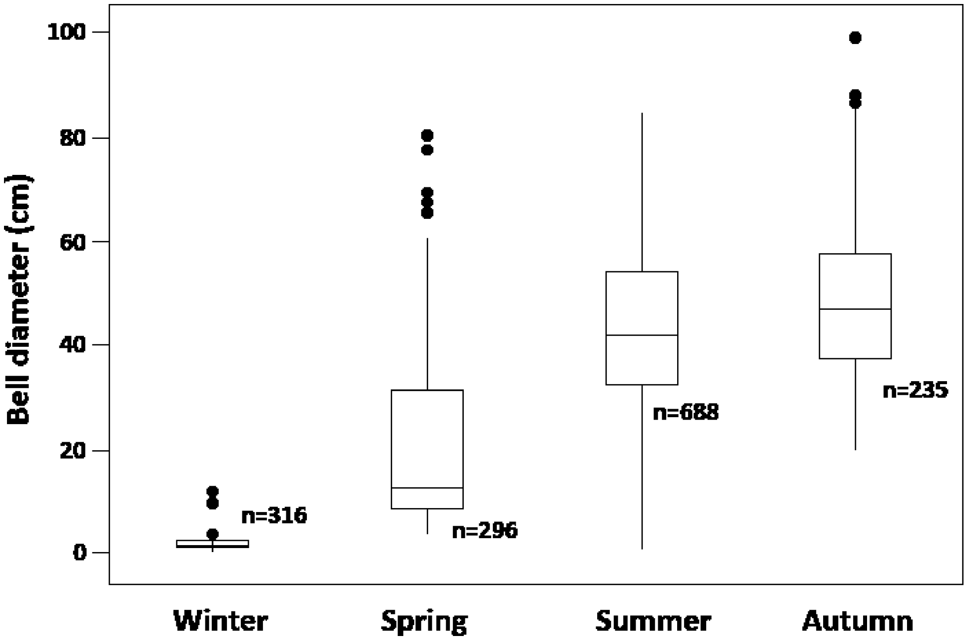

Figure 17 Boxplot of seasonal changes in bell diameter of *Chrysaora plocamia* off central Peru, from years 2007–2009 to 2012–2018 (No jellyfish were reported in 2016/2017). Lines within boxes represent the median, boxes represent the upper and lower quartiles and error bars represent the highest and lowest observed values. Small open circles represent outliers (Quiñones unpublished).

there is consistent decrease in body size, reflecting the protracted mortality of large medusae and possibly the recruitment of juvenile medusa by the end of summer (Ceh et al. 2015).

Biomass, growth and mortality

Biomass The length–mass relationship for *Chrysaora plocamia* was studied by Cáceres (2012) from individuals collected in two periods (2010/2011 and 2011/2012). These data are shown in Supplementary Table 1A. Although there are no region-wide estimates of jellyfish biomass, the biomass of *Chrysaora plocamia* was determined off the coast of Peru (from Punta Sal at ~4°S to the border with Chile, ~18°S) during a pelagic survey by IMARPE in summer 2009. The main objective of the cruise was to estimate the biomass of the Peruvian anchoveta, using multi-frequency hydroacoustics (SIMRAD EK60 echo sounder), which were supplemented with pelagic trawls and a Remotely Operated Vehicle. Echoview was employed to process the acoustic data collected and distribution was interpreted by kriging interpolation: biomass was determined from isoparalittoral stratification using areas of 10×30 nm (Simmonds & MacLennan 2005). The measurements of TS were carried out *in situ* when catches were comprised exclusively of *Chrysaora plocamia*. At a frequency of 120 kHz, target strength values between -84.9 and −66.15 dB were obtained (average −75.9 dB) for animals with a bell diameter of between 30 and 78 cm, and at a frequency of 38 kHz, the target strength values ranged between −84.8 and −63.0 dB (average −73.81 dB).

The distribution of *Chrysaora plocamia* was purely coastal and extended up to 12 nm offshore between Paita (5°S) and Punta Caballas (15°S). In the interior of Bahia Independencia (14°20′S), slightly smaller individuals with lower target strength values were recorded. At the 120 kHz frequency, biomass was estimated at 448,351 t with a confidence limit of 25.11%, while at the 38 kHz frequency, it was estimated at 382,153 t with a limit of 17.82%. Almost the entire abundance was found between 0 and 10 nm from the coast. Latitudinally, the largest biomass was located in the

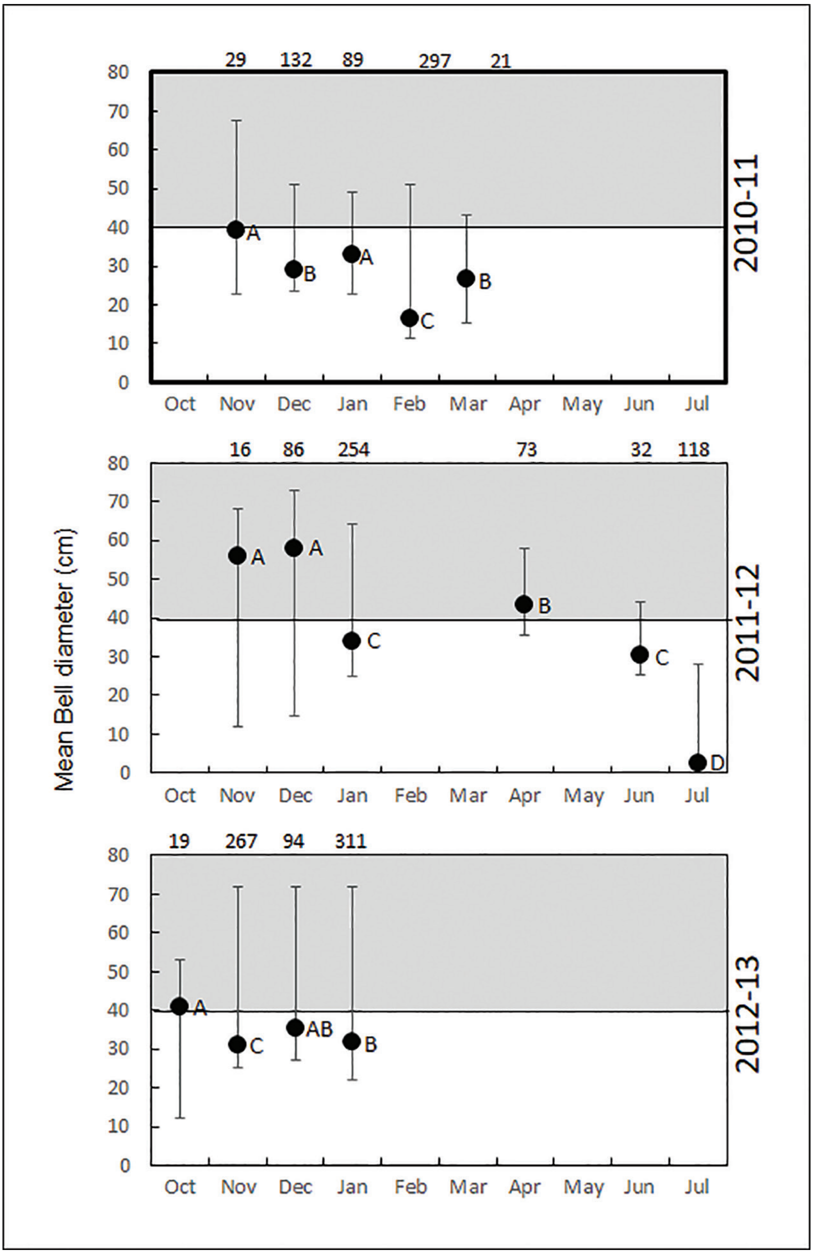

Figure 18 Monthly changes in mean body size of *Chrysaora plocamia* medusae during three years. Error bars show the maximum and minimum size. The black horizontal line represents the body size above which all animals were expected to be sexually mature. Different capital letters indicate significant differences between months (post hoc comparisons, Tukey-Kramer HSD). Numbers above panels represent the number of animals sampled (after Ceh et al. 2015).

area between Salaverry (8°S) and Callao (12°S). In general, the estimated biomass is an average of 410,000 t (biomass estimate of anchoveta ~8.2 million t) with the highest densities compared to Chancay and between Chimbote–Huarmey. The total extension area of *Chrysaora plocamia* during summer 2009 was 5410 km^2 (Castillo & Quiñones unpublished data).

Growth, mortality and longevity Estimates of growth rate for *Chrysaora plocamia* in Peru are lacking, although juvenile medusae grow rapidly from winter until summer, when most of the population consists of adult, sexually mature medusae (bell diameter: 40 cm; Ceh et al. 2015: Figure 18). Broadly similar results have been noted off Peru: the smallest individuals were noted in winter (mean 1.5 cm, $n = 316$), and these increased progressively through spring (mean 20.5 cm, $n = 296$) to reach a maximum in summer (mean 43.5 cm, $n = 688$) and autumn (mean 48.6 cm, $n = 235$) (Quiñones unpublished data).

Given the unusual dynamics of the *Chrysaora plocamia* population in Mejillones Bay, classical approaches to estimate the parameters of the von Bertalanffy growth function (i.e. modal progressions from length–frequency distributions) are not applicable. Therefore, Cáceres (2012) used the overall pooled length frequency distribution (Figure 19) for each year, which was subjected to

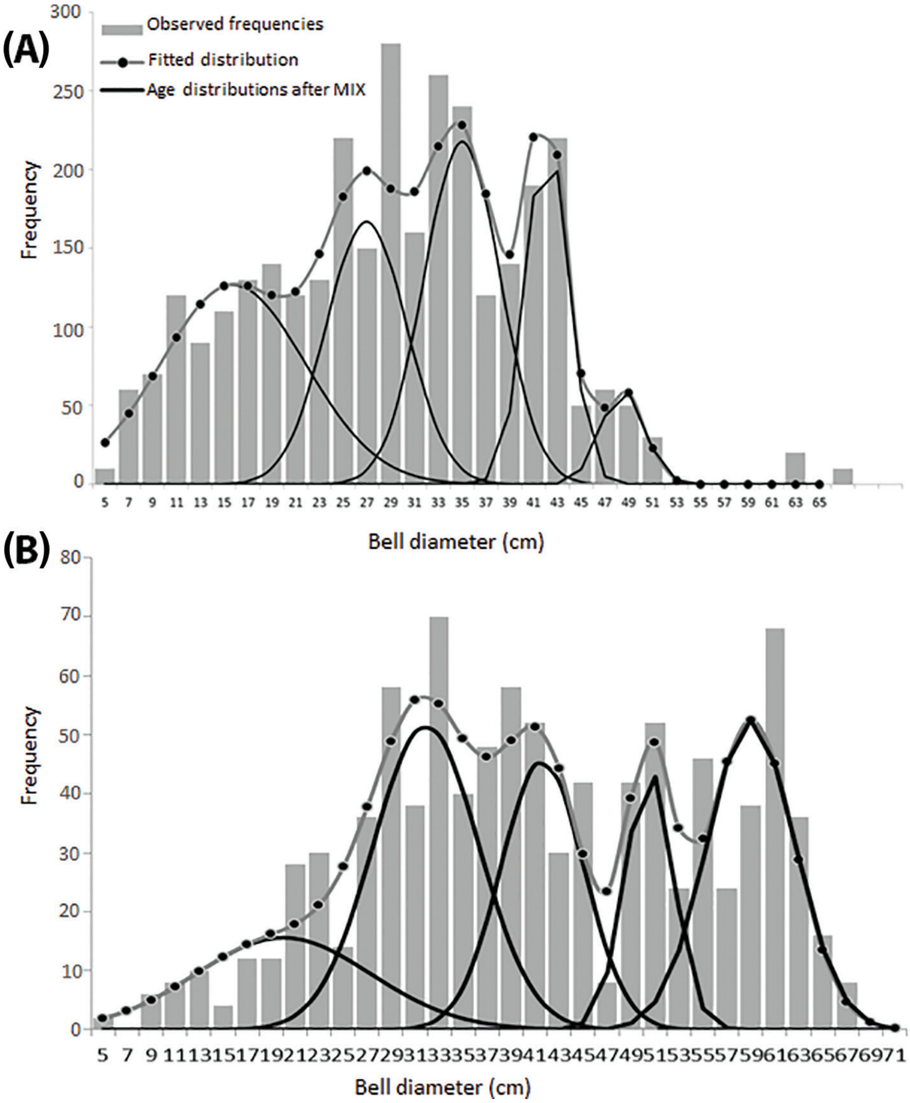

Figure 19 Pooled length–frequency distributions of *Chrysaora plocamia* for the season 2010/2011 (A) and 2011/2012 (B) with the fitting distribution from distribution mixture analysis and the resulting normal distributions of age groups (after Cáceres 2012).

distribution mixture analysis (Macdonald & Pitcher 1979) to decompose the mixture of age/length distributions into their separate components. These analyses indicated a slow growth ($K = 0.96$ yr^{-1}; $L_\infty = 80$ cm) for the year 2010–2011 and a faster growth ($K = 1.28$ yr^{-1}; $L_\infty = 80$ cm) for the year 2011–2012. For the same periods, total mortality (Z) was estimated by Cáceres (2012) using the single negative exponential model and a length-converted catch curve method (Pauly 1983) from pooled length frequency data. These estimations (Figure 20) indicated a much higher mortality for the first season (2010/2011), which was attributed to the higher abundance of *Chrysaora plocamia* during this season. Results on growth and mortality may also reflect interannual differences in climatic regimes in the area; the season 2010/2011 was characterized by strong, cold La Niña conditions in eastern Pacific in comparison with the season 2011/2012. Locally, these conditions may translate in increased upwelling strength and thus colder temperatures and increased food availability that may explain the combination of lower growth and higher abundance observed during this season.

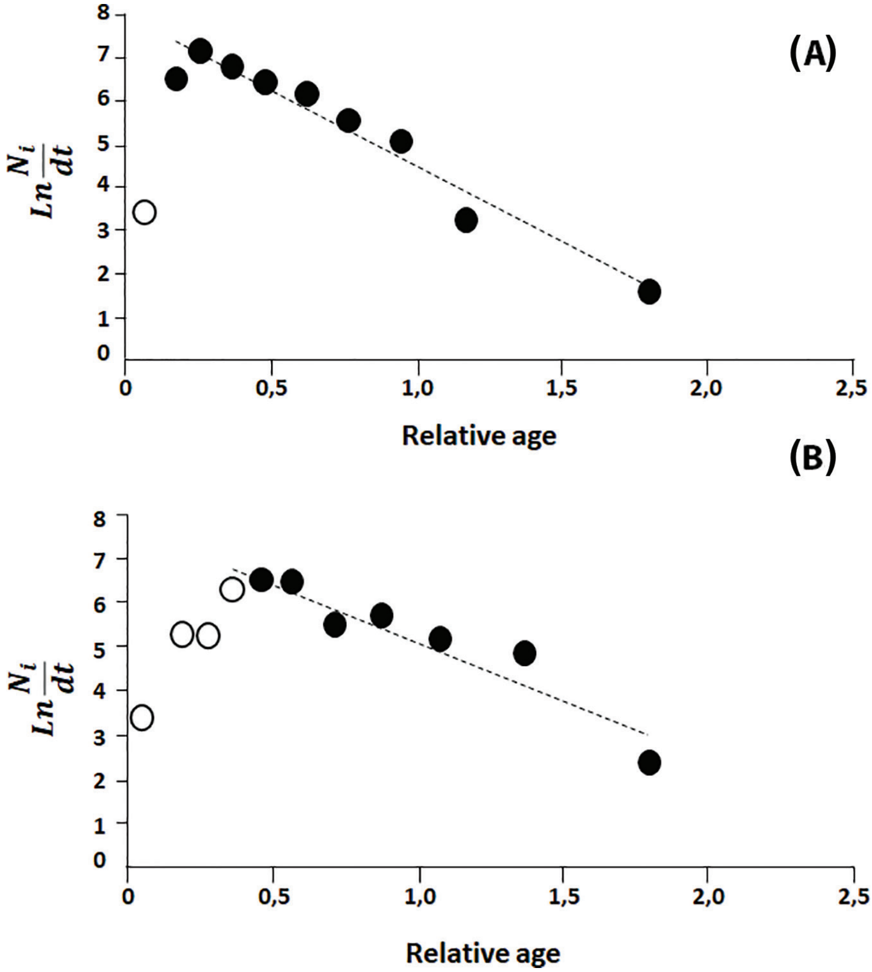

Figure 20 Estimations of total mortality for *Chrysaora plocamia* from length-converted catch curves for the season 2010/2011 (A) and 2011/2012 (B), based on pooled length–frequency data and the von Bertalanffy growth parameters. N_i is number in size class i, dt is the time required to grow through this size class. Filled data points used for regression, open data points excluded from regression. (A) $y = -3.498x + 7.969$, $r^2 = 0.945$, $Z = 3.498$; (B) $y = -1.993x + 7.516$, $r^2 = 0.887$, $Z = 1.993$.

Reproduction

Sexual Although a description of the full life cycle of *Chrysaora plocamia* is still pending (but see Morandini et al. 2013), it displays the typical metagenetic life cycle of most scyphozoans. *Chrysaora plocamia* is dioecious and presents no evident sexual dimorphism. Morandini et al. (2013) reported that mature medusae of *Chrysaora plocamia* may be caught in Ilo, southern Peru (17°S) during early November. Ceh et al. (2015) showed that sexually mature medusa (bell diameter ≥40 cm) occurs through the year when medusae are present in northern Chile, suggesting asynchronous reproduction.

Brood planulae are found within the long and spiralled oral arms and gastric cavity of fertilized females, and laboratory studies show that larvae will settle on available glass and plastic substrates from four to five days and metamorphose into whitish polyps. The settlement of planulae is influenced by temperature, suggesting that thermal anomalies observed during El Niño and La Niña affect the performance of settlement (Riascos et al. 2013a). Interestingly, it also appears that settlement is influenced by substrate colour, which may enhance polyp survival (Ceh & Riascos 2017).

Asexual No polyps of any Discomedusae have been observed *in situ* in the Humboldt region. Hitherto unpublished observations by Morandini and Schiariti at the University of São Paulo (São Paulo, Brazil) and INIDEP (Mar del Plata, Argentina) indicate that polyps reproduce asexually mostly by means of podocysts. Lateral budding has been also observed but only occasionally. Strobilation is polydiscal with the formation of a variable number of ephyrae (from 5 to 20) apparently depending on the size of the polyp. Although no specific studies have been performed, strobilation is regularly observed in cultures kept in darkness under constant conditions of temperature (20°C) and food supply (fed with newly hatched *Artemia* nauplii once weekly).

Riascos et al. (2013a) performed laboratory experiments to test for the effects of temperature on the performance of scyphistomae (polyps), observing that anomalous temperature regimes associated with El Niño-La Niña cycle, had a negative effect on somatic growth and survivorship of polyps of *Chrysaora plocamia*. This suggested that these fundamental processes perform better within the species-specific or even population-specific thermal tolerance limits related to their respective "normal" seasonal range of temperature.

The ephyrae (1–2 mm diameter) of *Chrysaora plocamia* have been described by Morandini et al. (2013) as translucent and have a purplish coloration; nematocyst warts can be found on the exumbrella at the base of each lappet. Fed a diet of scallops (*Nodipecten* – well let's face it who wouldn't!), the development of ephyrae/juvenile medusae is relatively fast and the first eight tentacles develop in just in two weeks at temperatures between 20 and 22°C; secondary tentacles appear after three to four weeks, and medusae reach a diameter of 5 cm in 45 days (Morandini et al. 2013). Detailed studies of ephyrae in plankton samples have not been undertaken in the region, although as noted previously they are assumed to be released during winter.

Interactions with other species and human activities

Diet

The dietary preferences and trophic roles of macromedusae in the Humboldt Current system is limited to the most abundant and conspicuous species of this system: *Chrysaora plocamia*. Using traditional gut content analysis, Riascos et al. (2014) counted and classified prey items found in the gastric cavities of 68 *Chrysaora plocamia* medusae (Bell diameter: 7–47 cm) collected from Mejillones (23°S, northern Chile) during summer (November 2010) and spring (March 2011). Their findings indicate that holoplanktonic crustaceans and fish eggs and larvae are the major components of the diet (from 52% to ~96%). Aller (2018) analysed the gut content of 35 adults (bell diameter: 23–65.5 cm) of *Chrysaora plocamia* from south-central Peru (Bahía Independencia, 14°S) during a warm El Niño episode and found that prey items comprised mostly zoea larvae (81%) and fish eggs

(6%, Mugilidae). It is important to highlight that these differences could be related to different environmental conditions, because while the Chilean study coincided with periods when SST anomalies were negative (–1.3°C), the Peruvian one was associated with positive anomalies (+1.9°C). In addition, these results could be related to a spatial component in prey availability. Despite the small scale of the studies conducted, the results provided by Aller (2018) show that *Chrysaora plocamia* are capable of feeding on a wide prey spectrum depending on environmental or biological factors.

Our knowledge of the dietary patterns of *Chrysaora plocamia* could be biased due to the fact that medusae have been collected only in surface waters during daytime. There is evidence to suggest that *Chrysaora plocamia* may be able to exploit both pelagic and benthic resources, reflecting unrecognized life-history traits (see Riascos et al. 2015). A diverse assemblage of benthic and benthic-emergent prey items has been noted in the gut of *Chrysaora plocamia* medusae, which could reflect the overwintering of adult medusa near the seafloor (Ceh et al. 2015). Alternatively, given that animals were sampled from a relatively shallow area (~50 m), it has been suggested that the vertical movements of predator and/or prey as well as the suspension of prey by bottom currents may contribute to the observed results (Ceh et al. 2015).

Parasitism

The hyperiid amphipod *Hyperia curticephala* has been described associating with medusae of *Chrysaora plocamia* in the Paita Bay (northern Peru) and Mejillones Bay (northern Chile) (Oliva et al. 2010, Riascos et al. 2015). Riascos et al. (2015) reported a high number of amphipods per host (median = 388; range 112–993). Associations between hyperiid amphipods and medusae are complex and vary greatly in timing, in the degree of host dependence (shelter and/or food) and the extent of maternal care (Gasca & Haddock 2004). The presence of small portions of mesoglea in the gut contents of all amphipods dissected by Oliva et al. (2010) suggests that *Hyperia curticephala* uses *Chrysaora plocamia* not only as substrate in the pelagic realm, but also as a food source (Oliva et al. 2010). Interestingly, this hyperiid was also observed parasitising medusae of the hydrozoan *Aequorea* sp. during the months when *Chrysaora plocamia* was scarce (April).

Another parasitic association has been documented by Riascos et al. (2013b) involving *Chrysaora plocamia* medusae and the sea anemone *Peachia chilensis*. These authors studied temporal patterns of parasite intensity biomass and the distribution pattern of parasites among hosts and found that the percentage of medusae harbouring larval actinians was high, fluctuating from 100% in November to 67% in March. They also observed that the host size is correlated with the intensity of infestation only in certain months suggesting that when parasite loads are high, space or other resource within the host may impose limits for further increases in parasite load. Riascos et al. (2013b) concluded that the parasite-induced host mortality and reduction of fecundity, represented by parasitic castration, are restricted to a few hosts and are therefore under the expected levels that characterise the dynamic equilibrium of host–parasite systems (Riascos et al. 2013b).

Predation

There is little empirical evidence of jellyfish predation in the Humboldt Current system. That said, *Chrysaora plocamia* forms part of the diet of some sea turtle species (Hays et al. 2009) and three of the five turtle species reported in Peruvian waters feed specifically (leatherback turtle, *Dermochelys coriacea*), or at least opportunistically (green turtle, *Chelonia mydas agassizii*, and olive ridley, *Lepidochelys olivacea*), on medusae (Goya et al. 2011, Quiñones et al. 2010). The biomass of medusae appears to be sufficient to support *Chelonia mydas agassizii* in the region (Quiñones et al. 2010).

Although the centrolophid fish *Seriolella violacea* has been shown to eat large quantities of jellyfish (including salps, pyrosomes and ctenophores; Mianzan et al. 2014), it is clear that the amphipods that parasitize *Chrysaora plocamia* are an important food source for the fish too (Riascos et al. 2012). Riascos et al. (2012) observed that juvenile *Seriolella violacea* prey exclusively on the hyperiids and not on their jellyfish host, suggesting that the relationship between fish and jellyfish is a facultative mutualism: juvenile fish obtain food and probably also protection from the medusa, whereas the medusa benefits from parasite removal: *Chrysaora plocamia* is a passive host, and *Seriolella violacea* is an active opportunist. However, this relationship changes to a predator–prey one with increasing fish size because larger fish eat both jellyfish and hyperiids (Riascos et al. 2012). It is interesting to note that when *Hyperia curticephala* parasitises the hydrozoan *Aequorea* sp., the number of hyperiids in the stomach contents of fish was negligible. This suggests that the timing of the association between fish and jellyfish may depend on the opportunities for preying on large quantities of densely aggregated hyperiids, as suggested by Mansueti (1963) for most fish–jellyfish associations.

Humans must also be considered as predators of jellyfish in the Humboldt Current system, because Mianzan et al. (2014) have reported Peruvian artisanal fishermen using the gonads of *Chrysaora plocamia* as bait to catch *Seriolella violacea*. Senescent or dead *Chrysaora plocamia* resting on the seabed have been observed being eaten by a variety of crabs (*Hepatus chilensis*, *Platymera gaudichaudii* and *Canary Currenter plebejus*) in both Independencia Bay and Puerto Eten (~7°S).

Jellyfish are involved in different biological associations other than trophic interactions (e.g. Ohtsuka et al. 2009), and numerous invertebrate taxa utilize *Chrysaora plocamia* as a substrate within the structureless water column. The large bell and conspicuous oral arms may also provide shelter and food for schools of juvenile starry butterfish (*Stromateus stellatus*) (Elliot et al. 1999).

Fisheries and human activities

Off the coast of Iquique (~20°S) in northern Chile, massive strandings of *Chrysaora plocamia* have occurred in the last two decades, and these have had far-reaching impacts on the local economy (Mianzan et al. 2014). The stings caused by jellyfish to bathers have caused the closure of some beaches, with the consequent effects on tourist activity during peak summer periods (January–February) (Mianzan et al. 2014; Riascos unpublished data).

Significant salmon farming operations are located around Chiloe Island in Patagonia, and when large numbers of *Chrysaora plocamia* occur in coastal waters there, the effects to the industry are severe. Such was witnessed between February and June 2002, when a bloom of jellyfish clogged and destroyed the nets of the culture cages, and pieces of jellyfish tissue penetrated the cages to contact and damage fish gills, causing starvation and mortality (Mianzan et al. 2014, Palma et al. 2007).

However, it is with commercial and artisanal fisheries that jellyfish impacts are the greatest. The high productivity of the northern Humboldt Current system supports one of the largest mono-specific fisheries in the world (Chavez et al. 1999, 2008, Pennington et al. 2006), making one of the largest contributions to the world fishery (Bakun et al. 2010). A fleet of >1200 industrial purse seiners operate along the coast at an industrial level (Fréon et al. 2008) and annually capture more than five million t of the Peruvian anchovy *Engraulis ringens* (FAO 2016). As noted previously, the environment of the northern Humboldt Current system is characterized by interannual and interdecadal fluctuations, with *Chrysaora plocamia* being a conspicuous member of the coastal fauna during the summer (Quiñones 2008, Quiñones et al. 2010, 2015). When the distribution of *Chrysaora plocamia* overlaps with that of anchovies (Ganoza et al. 2000, Bertrand et al. 2004), the jellyfish by-catch generates economic losses mainly to artisanal and industrial purse seine fisheries. These incidental catches are particularly problematic during pre-ENSO warm phases when *Chrysaora plocamia* is abundant, since fishermen have many problems finding waters without jellyfish in which to operate.

At broadscales, jellyfish by-catch increases sharply during El Niño periods and other warm events mainly within a warm El Viejo regime (Quiñones et al. 2010, 2015) when a simple fishing operation or set can capture over 100 t of *Chrysaora plocamia*. Economic losses to commercial operations will therefore be much greater in years of high jellyfish abundance, when the volume of jellyfish can be increased by up to 400% (Quiñones et al. 2018).

More locally, the oceanographic dynamics of the Peru–Chile elbow produce insolation warming in the zone between southern (17°S) and northern Chile (20°15′S), whereby very little cloud cover leads to surface warming mainly in spring and summer (Takahashi 2005). These processes are not necessarily linked to El Niño, but rather to Rossby tangential waves (Kiladis 1998), which originate in the central Pacific and propagate to impact the Peru–Chile elbow area. This localized warming, and the ingress of subtropical waters with elevated iodine concentrations, could trigger asexual reproduction of *Chrysaora plocamia* [polyps], which in turn can produce large blooms that can then interact with fishing. When abundant, medusae of this species interact (mainly) with the purse–seine fisheries and have a negative economic impact on the anchovy fishery. For instance, in southern Peru, 4% of the total industrial catch was discounted in the processing plants as a result of being mixed with *Chrysaora plocamia*. When jellyfish by-catch exceeded 40%, the whole catch was discarded, including anchovies. This occurred 13 times in the port of Ilo (17°38′S) with a total discard of ~387 t. When the deduction of USD160 per ton landed (jellyfish and anchovies discarded = 1268 t) was applied, the total estimate exceeded USD200,000 over 35 days with an average loss per boat of USD5 466 (Quiñones et al. 2013). Extrapolating these results, the economic loss for the entire jellyfish season (November–May) (Quiñones 2008) is ~USD1.2 million, with a national annual loss of ~USD7.1 million (Quiñones 2018). This would be a fairly moderate figure if we compare it with other ecosystems in which annual loss values between 10 and 40 million USD have been calculated (Kim et al. 2012, Palmieri et al. 2014). However, these losses are substantial in a country with economic limitations. In Northern Chile, between Arica (18°30′S) and Antofagasta (23°40′S), medusae of *Chrysaora plocamia* can become abundant during summer, and the species is constantly recorded as by-catch in the industrial purse seine pelagic fishery, according to reports of some governmental organisations.

Jellyfish not only interact with industrial fisheries in the Humboldt Current system, but also impact artisanal fisheries, which in Peru are extensive and numerous: there being more than 100 landing points, more than 9500 boats with a total population of 37,000 fishermen (Alfaro-Shigueto et al. 2011). Total landings approximate 500,000 t annually (Alfaro-Shigueto et al. 2010), which are much higher than the industrial landings of many countries (FAO 2016). In one pilot evaluation, carried out only in the port of Pisco (~14°S), a loss of USD27,500 was determined for the entire season of *Chrysaora plocamia*, so theoretically losses of the order of USD2.7 million could occur along the entire Peruvian coast (Quiñones 2018). It should be noted that this estimate was derived during a neutral phase of the Oceanic Child Index (ONI) (see NOAA 2020), when the seasonal abundances of *Chrysaora plocamia* are intermediate (Quiñones 2018). It is expected that economic losses for fishermen would increase significantly during WEs. It should be emphasized that the above cited case studies encompass a relatively short time period, both were pilot studies in artisanal and industrial fisheries; therefore, to estimate the impact that could occur on a larger scale, more studies would be needed and different scenarios should be considered.

Macromedusae in ecosystem models

The pelagic foodweb of the Humboldt Current system, being one of the most productive marine ecosystems in the world, has been modelled extensively using different approaches (e.g. Walsh 1981, Jarre & Pauly 1993, Carr 2001, Neira & Arancibia 2004, Taylor et al. 2008). However, only a few ecosystem modelling studies for this system have included gelatinous zooplankton (e.g. Moloney et al. 2005, Tam et al. 2008, Neira et al. 2014), and just one study have incorporated a macromedusae (*Chrysaora plocamia*) as a functional group (Chiaverano et al. 2018).

Our knowledge of the ecological role of macromedusae in the Humboldt Current system is limited to the large jellyfish *Chrysaora plocamia* in the northern section of the Northern Humboldt

Current System. Using empirical data of biomass (Quiñones et al. 2015) and diet composition (Aller 2017) of *Chrysaora plocamia* from Peruvian waters, Chiaverano et al. (2018) adopted a steady-state trophic model for the northern Humboldt Current system, previously developed by Tam et al. (2008), to quantify the efficiency of macromedusae and forage fish (anchovies and sardines). Their modelled foodweb of the northern Humboldt Current system indicated that forage fish represent the most efficient, direct energy pathway from primary and secondary producers (i.e. phyto- and zooplankton) to top-level consumers, while macromedusae act as an energy-loss pathway, by diverting energy from plankton producers away from higher trophic-level consumers and towards several low and mid-trophic-level consumers, such as planktivorous fish (mostly butterfishes) (Figure 21). Hence, during macromedusae blooms in this system, the total system ecosystem production being transferred upwards in the foodweb is expected to be reduced compared to non-bloom scenarios,

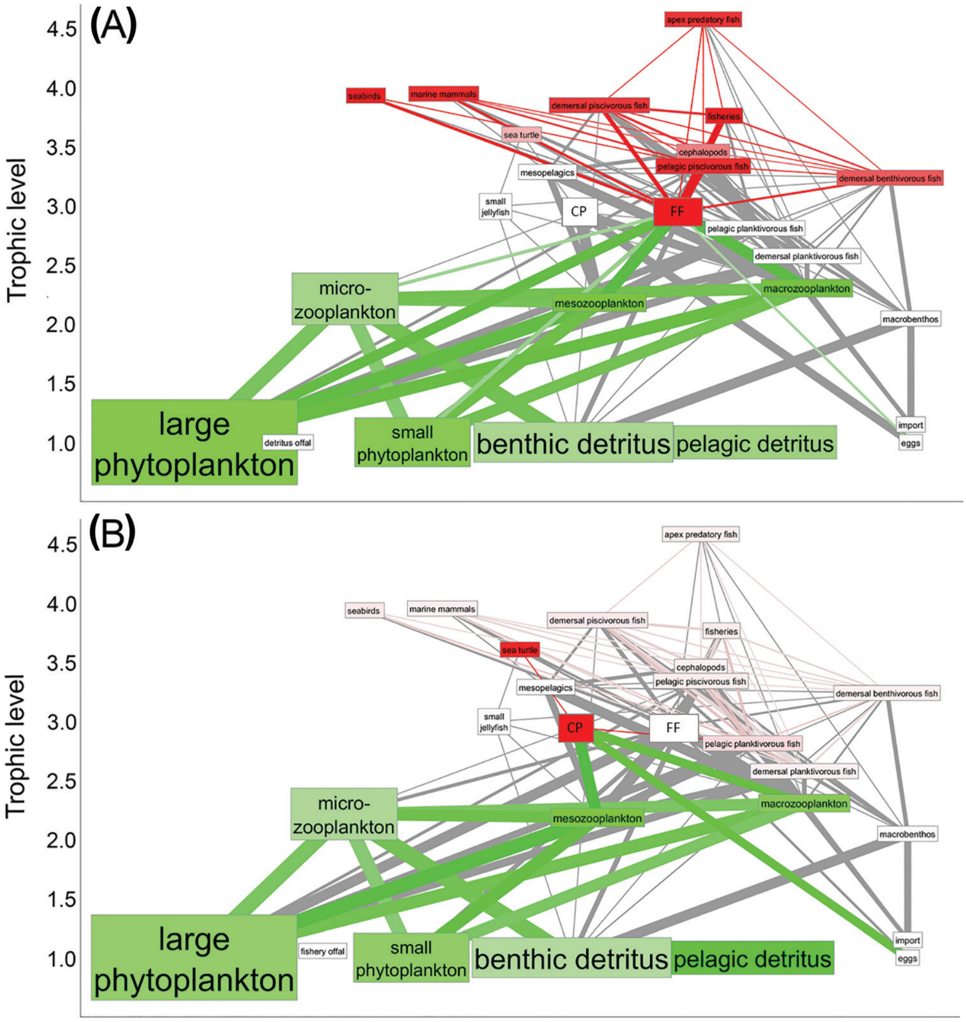

Figure 21 Modelled food web diagrams, highlighting energy flow patterns to (green) and from (red) forage fish (FF, A) and *Chrysaora plocamia* medusae (CP, B) in the Northern Humboldt Current system. Box size is proportional to functional group biomass. Colour intensity and width of lines are scaled to the amount of energy flow between forage fish and large jellyfish and the rest of the functional groups (modified from Chiaverano et al. 2018).

when forage fish dominate. These patterns are in congruency with those observed in the Northern California Current system (Ruzicka et al. 2012), supporting the role of forage fish and macromedusae as energy conduits and production-loss pathways, respectively, in marine ecosystems (Robinson et al. 2014). Interestingly, macromedusae represent a direct energy pathway to sea turtles (mainly leatherbacks) in the northern Humboldt Current system (Figure 21), highlighting the potentially important ecological role of macromedusae in the conservation of endangered, gelatinivorous marine reptiles (Paredes 2015, Quiñones et al. 2015), not only in this area, but in pelagic ecosystems worldwide.

In the northern Humboldt Current system, forage fish, macromedusae and forage fish fisheries appear to be interlinked. Through the use of modelled structural scenarios, Chiaverano at al. (2018) shows that an increase in macromedusae consumption translates into a decline not only in forage fish production, but also in the productivity of almost all mid-trophic- and upper-level consumers, with the exception of sea turtles (Figure 22A). On the contrary, a decline in macromedusae productivity occurs as a result of an increased forage fish consumption (Figure 22B). Forage fish and *Chrysaora plocamia* medusae are known to exhibit diet overlap (Espinoza & Bertrand 2008, Espinoza et al. 2009, Riascos et al. 2014, Ceh et al. 2015, Aller 2017); thereby, during macromedusae blooms, a reduced prey availability to forage fish can have strong subsequent effects throughout the entire ecosystem, considering how important forage fish are at transferring energy through the foodweb.

Interestingly, structural scenarios indicate that fisheries production can also be negatively affected by an increase in macromedusae consumption in this system (Chiaverano et al. 2018) (Figure 21A). This observed effect is likely the product of the negative effect of macromedusae on forage fish productivity, presumably via resource competition (see above). In Peru, forage fish (anchovies and sardines) make up >95% of the country's annual fishery landings, with the Peruvian anchoveta (*Engraulis ringens*) accounting for 99% of total forage fish landings (FAO 2011). For instance, a 37% increase in macromedusae consumption leads a 13% decrease in fisheries production in Peru. Considering that the Peruvian anchoveta fishery is one of the largest fisheries in the world, with an average annual landing of 6.5 million t (FAO 2011 cf FAO 2016), a 13% decrease in productivity of this fishery translate to a decrease in ~845,000 t of fish. During large bloom events in the northern Humboldt Current system, *Chrysaora plocamia* can reach up to a biomass 2.9–6.4 times greater (Quiñones et al. 2015, 2018) than the scenario tested by Chiaverano et al. (2018); thereby, such events are expected to have a much higher negative impact on forage fish production, and consequently, on forage fish fisheries. Future modelling efforts will aim at assessing the effects of such large blooms on fisheries productivity.

Interactions among macromedusae, forage fish and fisheries can potentially have large effects on productivity of upper trophic levels, since a decrease in production of a key functional group like forage fishes can lead to a significant reduction in productivity of seabirds (Cury et al. 2011) and economically important pelagic fish (Pikitch et al. 2014, Smith et al. 2011). We recommend macromedusae to be explicitly included in future ecosystem modelling efforts in ecosystem-based approaches to fishery management of coastal ecosystems worldwide (Brodeur et al. 2016).

The California Current Ecosystem

Description

The West Wind Drift or Subarctic Current flows across the North Pacific and then bifurcates off North America to form the Alaska Current that flows to the north, and the California Current that flows to the south. The California Current extends from southern British Columbia to Baja California, approximately 50–~22°N. The California Current, as it streams equatorward, mixes with oceanic waters and with those from the south, and these water masses are also subsequently

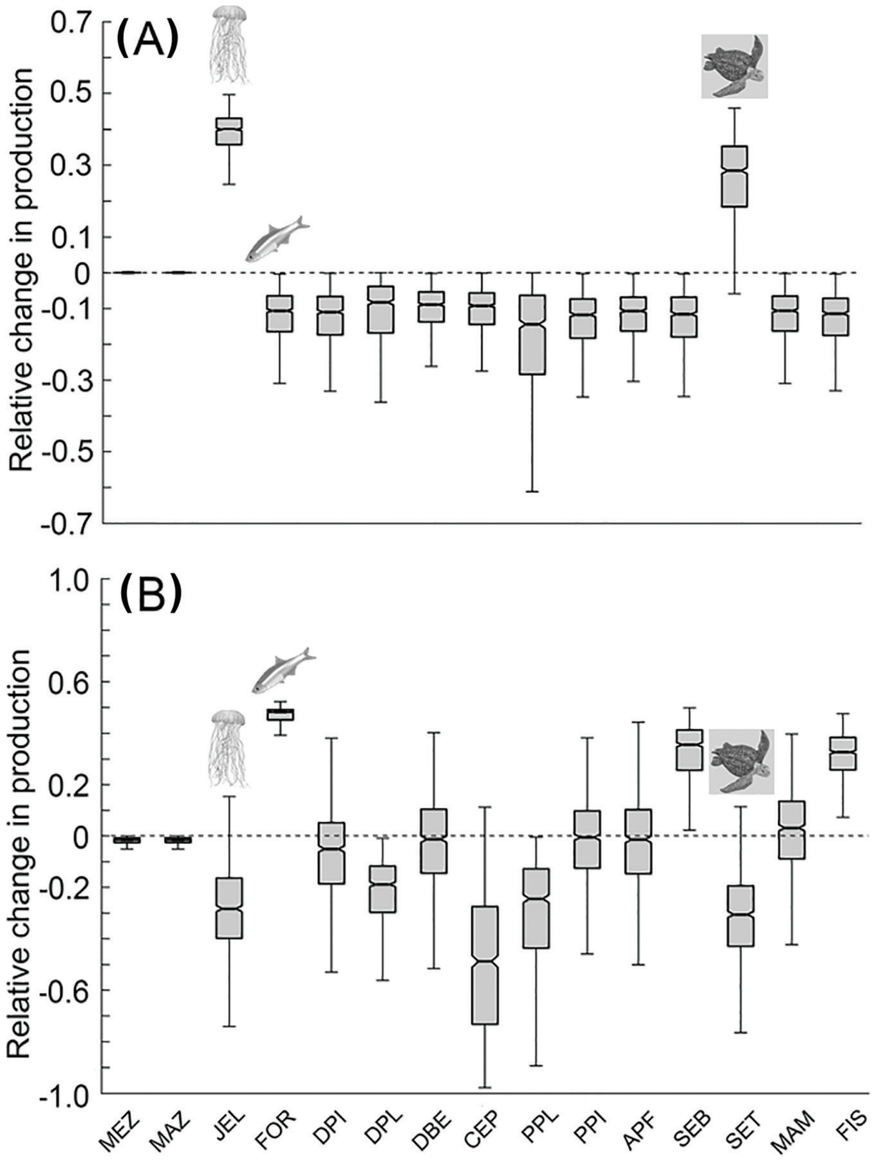

Figure 22 Ecosystem-wide responses to a modelled increased in *Chrysaora plocamia* medusae consumption (37%, A) and a forage fish consumption (50%, B). JEL: *Chrysaora plocamia*, FOF: forage fish, DPI: demersal piscivorous fish, DPL: demersal planktivorous fish, DBE: demersal benthivorous fish, CEP: cephalopods, PPL: pelagic planktivorous fish, PPI: pelagic piscivorous fish, APE: apex predatory fish, SEB: seabirds, TUR: sea turtles, MAM: marine mammals, FIS: fisheries. Box: 25%–75% quartile, whiskers: min–max. Notice different scale in *y*-axis (modified from Chiaverano et al. 2018).

modified by coastal processes such as runoff and upwelling in this EBC. Within the California Current, Checkley and Barth (2009) delineated three geographical regions based on a combination of biogeographic boundaries and wind stress which include (1) the northern region (40–48°N) where wind stress varies from poleward to equatorward, (2) the central region (34–40°N) with the strongest wind stress, mainly equatorward, and (3) the southern region (22–34°N) where wind stress is predominantly to the south (Figure 23).

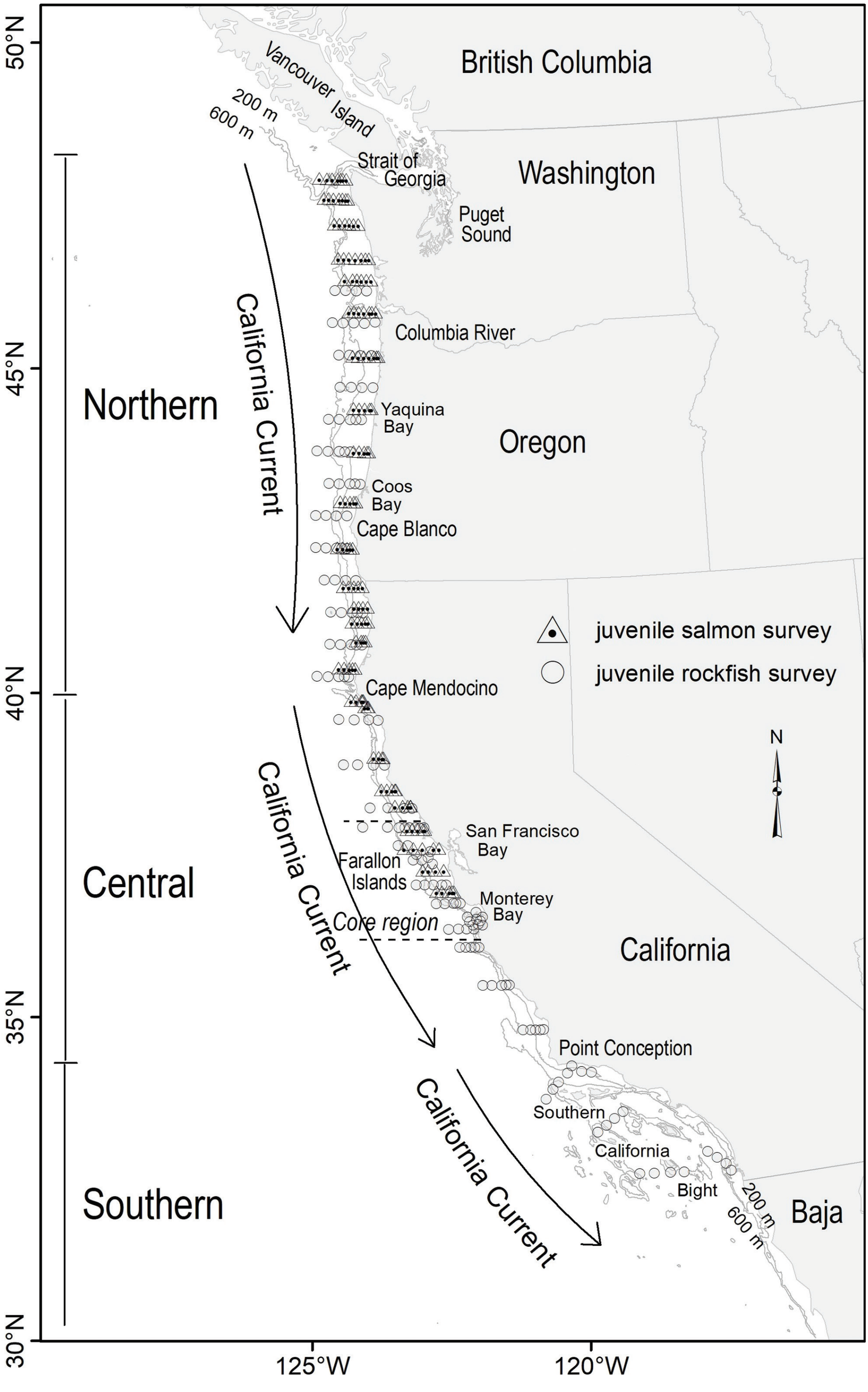

Figure 23 Main geographic features of the California Current showing stations sampled during the main research surveys along with geographic divisions used here.

These transitional regions in the California Current are highly dynamic and ocean conditions fluctuate widely over time and space. The regions have distinct seasonal as well as interannual and interdecadal fluctuations. In the northern California Current region, coastal upwelling is episodic off Oregon during summer, but more persistent off northern California. During the upwelling season, a coastal jet forms and dynamic frontal zones sometimes extend far out to sea. In winter off the Pacific Northwest coast, the California Current either moves offshore or is replaced by the poleward flow of the Davidson Current. The California Undercurrent is a subsurface poleward current generally confined to the continental slope and most intense during the summer (Hickey 1998). During El Niño events, the equatorward flow of the California Current is anomalously weak, and southern water intrusions move into region. Thus, interannual variations in the northern California Current result from both regional- and global-scale processes (Landry et al. 1989, Hickey 1998, Checkley & Barth 2009). Interdecadal fluctuations with periods of 15–25 years have also been documented in the North Pacific and in the coastal transition region (Hare & Mantua 2000). These were based on variations in sea surface temperatures and abrupt changes in the survival or species composition of pelagic animals, such as those which occurred in 1977 and 1989.

The oceanography of the central California Current varies considerably compared to that of the northern California Current (e.g. ocean waters offshore of Oregon and Washington coastlines) in several ways, some of which have relevance to pelagic jellyfish abundance and distribution. In the northern California Current, strongly seasonal upwelling winds during spring and summer and a relatively smooth coastline lead to the development of a strong coastal jet over the continental shelf, with variable but typically strong seasonal upwelling supporting high productivity. As that coastal jet develops around Cape Blanco, Cape Mendocino and other features towards the south, the jet as well as the offshore flow in the California Current begins to exhibit higher eddy kinetic energy, leading to a more complex mesoscale regime of jets, eddies and meanders due to coastal geomorphology and complex bathymetry (McClatchie 2014).

Strong upwelling centres are located adjacent to headlands; important regions of enhanced primary productivity occur downstream of these sites, many of which are characterized by substantial mesoscale (and finer scale) eddy activity and complex circulation patterns (Strub et al. 1991, Steger et al. 2000). Moreover, upwelling centres near headlands influence the production and spatial distribution of phytoplankton in relation to the continental shelf in both onshore–offshore and latitudinal dimensions. For example, within the central California Current, Largier et al. (2006) showed that upwelling centres are characterized by high-nutrient low-chlorophyll waters, with high chlorophyll waters located downstream from the upwelling centre. Furthermore, upwelling "shadows" exist along the coast in the lee of coastal headlands and capes; here, alongshore flow is reversed, and the retained water contains high concentration of chlorophyll and zooplankton (Graham et al. 1992, Graham & Largier 1997, Steger et al. 2000, Largier et al. 2006). These habitats are among the most important habitats for large pelagic Scyphomedusae in this region. In the Gulf of the Farallones, the upwelling shadow includes one of the widest areas of the continental shelf between Cape Blanco, Oregon (43°N) and Point Conception, California (34°30′N), such that there are approximately 50 km between shore and the shelf break in this region, relative to a coastal average closer to 20 km throughout most of the remaining coastline (Steger et al. 2000). Similarly, Monterey Bay is a widely recognized productive region for Scyphomedusae (among other organisms) due to its retentive circulation patterns and complex bathymetry (Graham & Largier 1997, Benson et al. 2007).

Most of the primary production in the California Current is generated by unicellular algae dominated by diatoms especially during upwelling, with dinoflagellates and cyanobacteria in more offshore and nutrient poor waters (Kudela et al. 2008). Grazers upon these phytoplankton are dominated by microzooplankton, copepods, euphausiids, pteropods and other small zooplankton, although in less productive waters, gelatinous forms such as appendicularians, salps and heteropods can become more important (Peterson et al. 2017). The next higher trophic level, microcarnivores, is dominated by micronekton such as larger crustaceans and squid, many larger gelatinous zooplankton including ctenophores, hydrozoans and scyphozoans, along with larval and juvenile fishes (Pearcy 1972, Brodeur et al. 2003). Similar to the other upwelling ecosystems, small pelagic fishes that consume primarily smaller planktonic prey including phytoplankton, copepods, pteropods, decapod larvae and juvenile euphausiids (van der Lingen et al. 2009, Brodeur et al. 2019a) can occur in high biomass (Zwolinski et al. 2012). The ability of small pelagic fishes such as sardines (*Sardinops sagax*) and anchovies (*Engraulis mordax*) to filter feed allows them to pass production on to higher trophic levels relatively efficiently. Finally, these small pelagic fishes and other micronekton become the main prey of a variety of larger pelagic and demersal fishes, seabirds and marine mammals leading to a highly productive marine ecosystem (Ware & Thompson 2005, Field et al. 2006).

Macromedusae

Species composition

One of the first studies to document gelatinous zooplankton from the northern California Current was the review of pelagic animals caught off Oregon from 1960 to 1968 by Pearcy (1972). He lists 33 Hydrozoa, 5 Scyphozoa, 2 Ctenophora, 1 Larvacea and 8 Thaliacea collected. “Coelenterates” had the second highest biomass after Copepoda of all the major zooplankton groups, including even the Euphausiacea, reflecting their importance in this region. Wrobel and Mills (1998) provide an overview of the gelatinous taxa found along the Pacific Coast of North America. Although many Scyphomedusae and Hydromedusae are known to occur in the California Current, we have restricted our coverage to the larger species that occur in relatively high abundances or are caught frequently in larger sampling gears. These include the scyphozoans *Chrysaora fuscescens* and *Chrysaora (Pelagia) colorata* (Family Pelagiidae), *Aurelia labiata* (Family Ulmaridae), *Cyanea capillata* (Family Cyaneidae), *Phacellophora camtschatica* (Family Phacellophoridae) and the large Hydrozoa *Aequorea* spp. (Family Aequoreidae). Representative photographs of these species are shown in Supplementary Figure 5.

In the California Current, early references of the moon jellyfish identified as *Aurelia aurita* are erroneous, and the species records should be regarded as *Aurelia labiata* (Mills & Larson 2007). Gershwin (2001) conducted an extensive morphological review of 17 populations of *Aurelia* from San Diego to Alaska and showed that all populations examined were attributable to *Aurelia labiata* and not *Aurelia aurita*. Mills & Rees (2007) have suggested that the smaller inshore specimens of *Aequorea* are likely to be the Northeast Pacific endemic species *Aequorea victoria*, but a second, larger oceanic species, possibly *Aequorea coerulescens*, may occur in coastal waters on a seasonal basis, and because of our inability to distinguish between the two species of *Aequorea*, we primarily refer to *Aequorea* as *Aequorea* spp. Finally, the main distribution of *Cyanea capillata* is somewhat north of the California Current, and although it is common in marginal seas at the same latitude such as the Salish Sea (Reum et al. 2009), it occurs relatively infrequently and in low abundance in the California Current and will only briefly be discussed in this review. Similarly, the subtropical species, *Chrysaora colorata*, is found only in the warmer regions of the California Current and is not very abundant, and thus much less studied, compared to the other species.

Distribution

Space Shenker (1984) analysed the Scyphomedusae from 263 fine-mesh purse seines made in the surface waters off Oregon and Washington from May through August of 1981. *Chrysaora fuscescens* was the numerically dominant species and occurred in >82% of the collections made, followed by *Aurelia labiata* (24.3%) and *Cyanea capillata/Phacellophora camtschatica* (22.4% combined). Densities of *Chrysaora fuscescens* were highest in a narrow band close to shore, especially during strong upwelling periods (Shenker 1984). *Aurelia labiata* were generally less abundant later in the summer and were found mostly between 10 and 15 km from shore. Pearcy et al. (1985) contrasted similar purse seine collections of gelatinous zooplankton from a strong upwelling year (1982) with that of an El Niño year (1983) and found that the frequency of occurrence of most of the large medusae with the exception of *Aurelia labiata* decreased the second year. Heitstuman (1994) conducted extensive surveys for medusae offshore by SCUBA diving and found few specimens during the 1993 El Niño, but they were more apparent during the more normal summer of 1994.

Extensive fine-mesh surface trawl collections ($n = 365$) from June and August of 2000 and 2002 from Central Oregon (45°N) to northern California (42°N) were characterized for their medusa composition by Suchman & Brodeur (2005). The dominant species caught were the scyphozoans *Chrysaora fuscescens*, *Aurelia labiata* and *Phacellophora camtschatica* and the hydrozoan *Aequorea* spp. The latter species showed the highest frequency of occurrence overall due to its broad cross-shelf distribution, but *Chrysaora fuscescens* and *Aurelia labiata* were substantially more important in terms of biomass especially inshore, whereas *Phacellophora camtschatica* was important only during the August cruise, mainly in the southern part of the sampling area. There were no day–night differences in catch based on some limited diel sampling (Suchman & Brodeur 2005). It was suggested that mesoscale physical features such as eddies and fronts may affect the distribution patterns of these weakly swimming organisms, leading to dense aggregations at convergent zones (Suchman & Brodeur 2005). There also seemed to be some larger-scale habitat partitioning among the dominant jellyfish species, with *Chrysaora fuscescens* being found closer to shore and at the more northerly stations, whereas *Aurelia labiata* were found more offshore and to the south of the sampling area.

Suchman et al. (2012) analysed interannual and seasonal variations in the abundance of large medusae from 1746 surface trawls off Oregon and Washington in the northern California Current over eight years (2000–2007). *Chrysaora fuscescens* and *Aequorea* spp. were caught in a similar proportion of the trawls (42% and 40%, respectively), but the abundance of the former, which peaked later in the summer, was an order of magnitude higher than the latter, which had a June peak in density. *Chrysaora fuscescens* tended to occur mainly at the innermost stations along each transect, while *Aequorea* spp. were more broadly distributed with their centre of abundance further offshore.

In the coastal waters of the central and southern California Current, relatively little focused research has been conducted on large medusae. One of the first accounts for this region have noted that blooms have been historically described as frequent events in this region over time, such as the account of Galigher (1925), who noted "the hordes of jellyfish which appear annually along our shores". Graham (1994) conducted a rigorous evaluation of the distribution of swarms of *Chrysaora fuscescens* in Monterey Bay relative to persistent hydrological features (upwelling shadows) and the swimming behaviour that led to the characteristic swarms that are commonly encountered in coastal regions of the southern California Current. Some of the data from Graham (1994) were derived from an ongoing survey of juvenile rockfish and other micronekton in central California waters. Since 1983, the Rockfish Recruitment and Ecosystem Assessment Survey (RREAS), using a modified Cobb midwater trawl, has been conducted in the waters off central California during the spring (May–June) upwelling season to sample the abundance and distribution of juvenile rockfish and other young-of-the-year fishes and forage species (Lenarz et al. 1995, Ralston et al. 2013, Sakuma et al. 2016). The initial survey area was along the Central California coast (~36–38°N); however, the range of the survey was expanded to cover most or all California waters starting in 2004. Although not the target of the survey, jellyfish have been integral to the survey since its inception (Graham 1994). Data on the species composition and abundance of the three most frequently encountered large scyphozoans (*Chrysaora fuscescens*, *Aurelia labiata*, *Chrysaora colorata*) have been collected reliably since 1990 (occasionally before then), with the exception of the years 2002 through 2004, and have begun to yield insights regarding the distribution, year-to-year variability and ecosystem interactions of these species in this region. Data on the abundance of *Phacellophora camtschatica* have been collected since 2009.

Due to the large-scale biogeographic features and circulation patterns described earlier, the central California region also appears to be the region of greatest relative abundance of these scyphozoan species, as illustrated by mean catch rates over the broader southern California Current survey range using data available from 1990 through 2019 (Figure 24). The two more abundant species of scyphozoans, *Chrysaora fuscescens* and *Aurelia labiata*, have their greatest relative abundance in nearshore central California waters, particularly the Gulf of the Farallones and Monterey Bay, with *Chrysaora fuscescens* more frequently found in offshore waters to the north and south of this

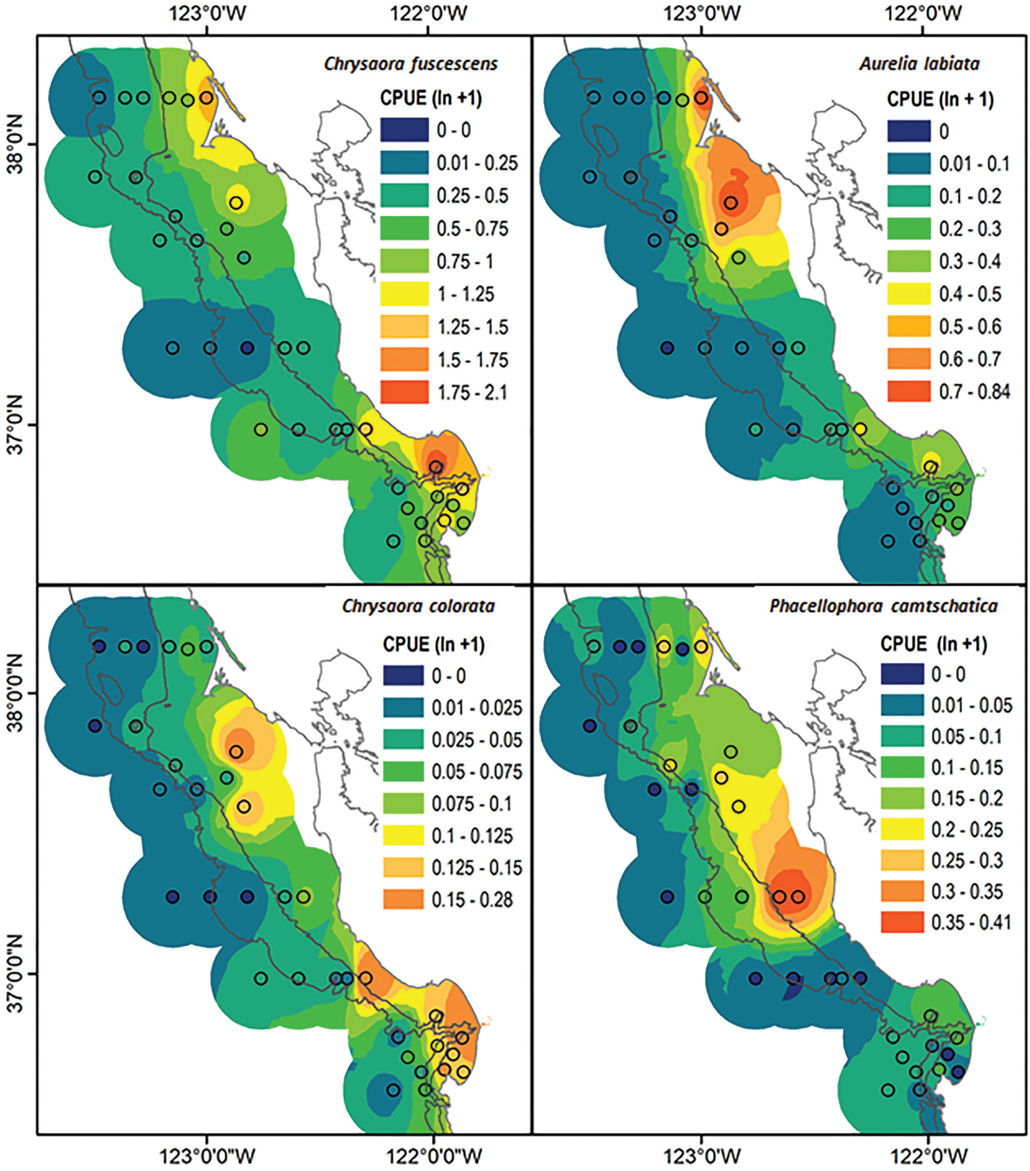

Figure 24 Average catch per unit effort (CPUE) of the four dominant Scyphomedusae using the core area climatology from 1990 to 2019 (note jellyfish were not recorded from 2002 to 2004). Circles represent the catch for stations ($n = 35$) that were sampled 13 or more times in the 27 years of sampling. Note that the range of catches are different for each species to indicate relative catch within species.

region. The next species, *Chrysaora colorata*, a solitary rather than swarming species, has a similar distribution but is considerably less abundant than the first two, although it is more abundant in nearshore waters (Figure 24). Finally, *Phacellophora camtschatica*, another non-aggregating species, has a centre of distribution situated between the peaks of the other species (Figure 24).

Since 2013, the RREAS has been expanded to include much of the northern California Current from southern Washington to the U.S.A – Mexico border (Figure 23), using similar methodology throughout (Miller et al. 2019). The annual distributions of the previous four species and *Aequorea* spp. show substantial broadscale overlap in many years (Figure 25). *Chrysaora fuscescens* showed centres of abundance at the northern end of the survey and in Monterey Bay, with lower abundances in between (Figure 25A). A similar distribution pattern was observed for *Aurelia labiata*, with the exception of slightly higher abundances off Cape Mendocino in the latter two years (Figure 25B). In contrast, *Phacellophora camtschatica* were caught in much lower abundances and were more broadly distributed along the coast both inshore and offshore (Figure 25C). The distribution of *Chrysaora colorata* was confined to south of Cape Mendocino in all but the warm year of 2017 and was close to shore in most years (Figure 25D). The large hydrozoan *Aequorea* spp. was generally most abundant in the northern part of the northern California Current (although they were not quantified off California prior to 2016) and were particularly abundant in 2015 during the first year of the marine heatwave (Figure 25E).

With respect to scyphozoan distribution patterns, Santora et al. (2012) evaluated 20 years of abundance data from the core area of these coastwide surveys to evaluate distribution and species association patterns of a suite of marine micronekton sampled in that survey (juvenile groundfish, forage fishes, krill, squid and jellyfish) off central California. They found that mesoscale variability of ocean conditions is the principal driver behind the spatial organization of the micronekton assemblages, with regions of species assemblages correlated to physical factors, latitudinal differences and the influence of localized upwelling and retention patterns. In other words, jellyfish distribution patterns, like those of other micronekton in this ecosystem, are largely defined by bathymetric and physical patterns, with centres of upwelling and relaxation leading to distinct micronekton assemblages (Graham 1994. Graham et al. 2001, Santora et al. 2012). For example, the retention areas north and south of Point Reyes typically included high numbers of the jellyfish (primarily *Chrysaora fuscescens*), resulting in strong loading with respect to spatial overlap patterns with the krill *Thysanoessa spinifera* and juvenile salmon (*Oncorhynchus* spp.).

A comparison of the large-scale macromedusae distribution in cool and warm ocean conditions was made from the early summer (June and July) surface trawl collections described by Suchman et al. (2012) but expanded to include a similar survey off southern Oregon and northern California (Harding et al. 2011). Distribution maps were made from the stations shown in Figure 23 for a seven-year period which included three cool years (2011–2013) and four warm years (2010, 2014–2016) for the dominant species (Figure 26). The dominant inshore species, *Chrysaora fuscescens*, showed three main centres of distribution (off Washington, southern Oregon and off central California) during both warm and cool years, and although their abundances were somewhat higher during the cool years, they were not significantly more abundant than the warm years (Figure 26). *Aurelia labiata* tended to be more abundant and widespread during warm years and tend to occur in more offshore waters than *Chrysaora fuscescens* (Figure 26). The largest macromedusae species, *Phacellophora camtschatica*, tended to be distributed the furthest offshore, and was significantly more abundant in warmer years especially south of Cape Mendocino (Figure 26). In contrast, *Cyanea capillata* was found almost entirely north of Cape Mendocino and showed no significant differences between cool and warm years. Finally, the Hydromedusa, *Aequorea* spp., was more broadly distributed and significantly more abundant in warmer years especially closer to shore (Figure 26).

Data from across Puget Sound, an adjacent inland sea which forms a major part of the Salish Sea together with the Strait of Georgia, show that large jellyfish are a major portion of pelagic biomass and that spatial heterogeneity exists in the relative abundance of jellyfish and small pelagic

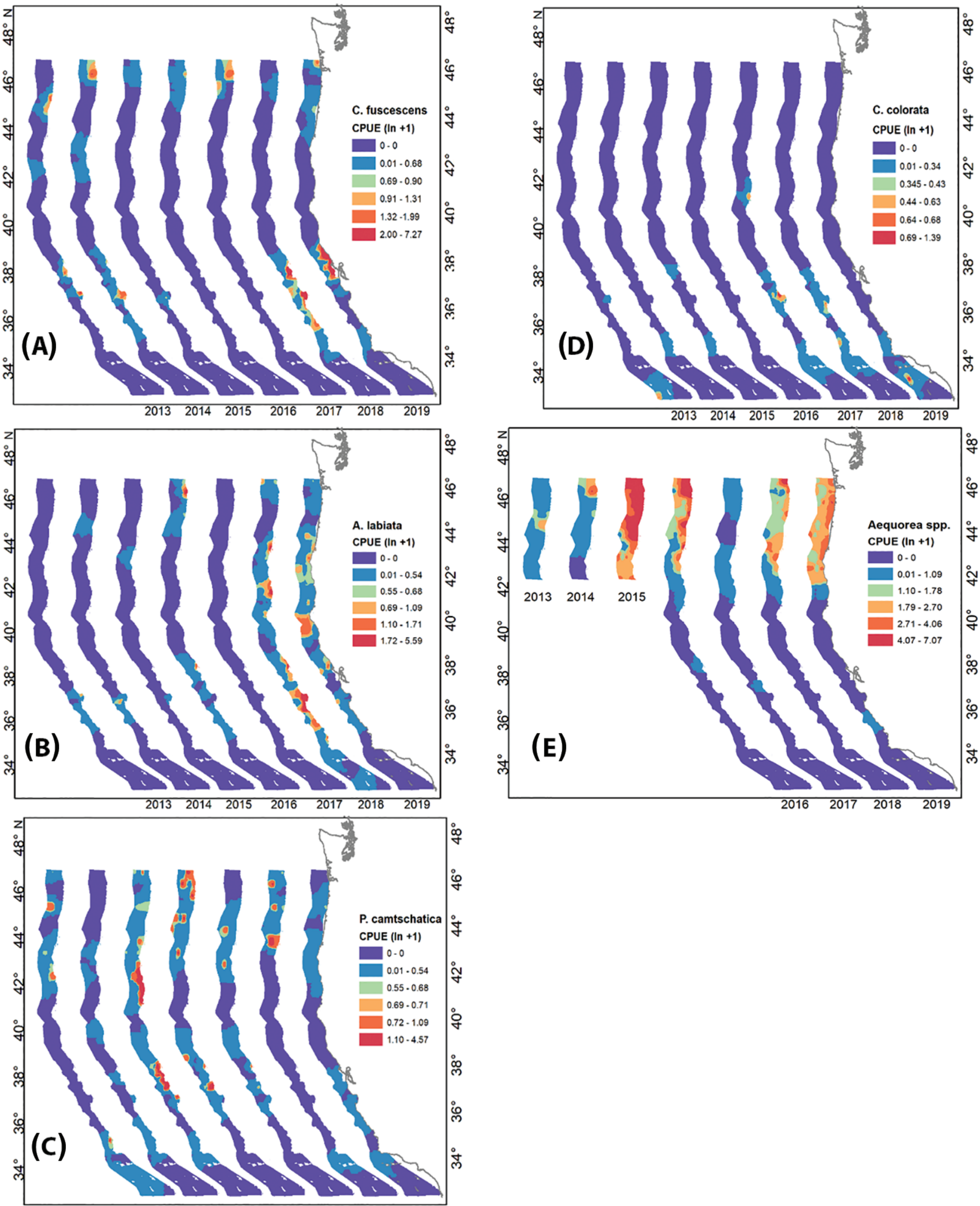

Figure 25 Relative abundance (log of the average numbers of individuals per haul) of (A) *Chrysaora fuscescens*, (B) *Aurelia labiata*, (C) *Phacellophora camschatica*, (D) *Chrysaora colorata* and (E) *Aequorea* spp. in the California Current in the May–June period, from 2013 to 2019. See Figure 23 for location of sampling stations. No data for *Aequorea* spp. were collected south of 42°N during the first three years. Classifications are based on the quantile distribution of positive catches (0; 0.01%–19%; 20%–39%; 40%–59%; 60%–79%; 80%–100%)

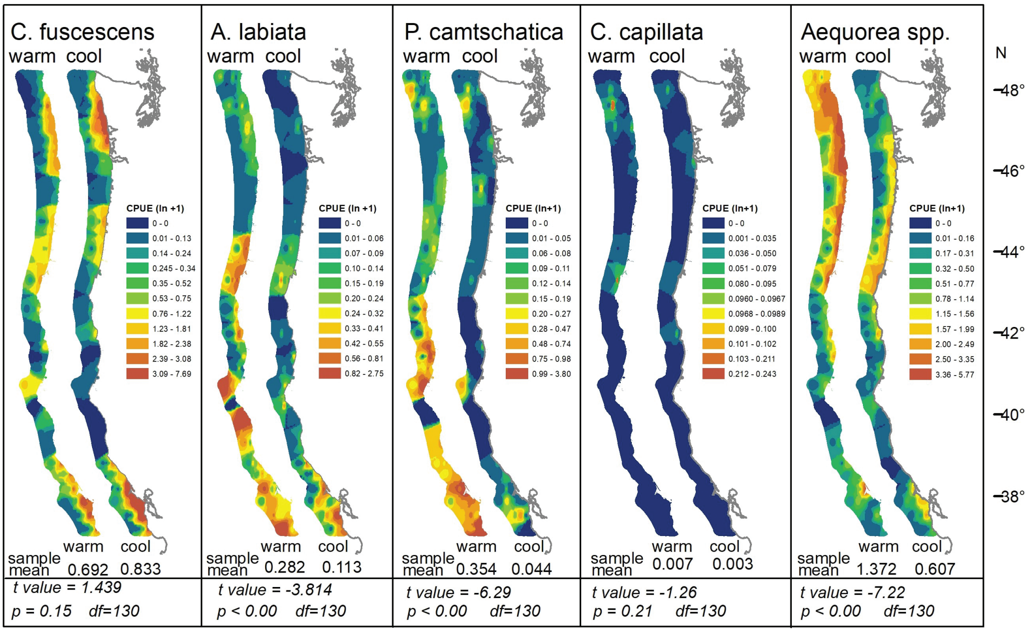

Figure 26 Large-scale distribution maps for the dominant macromedusae for cool (2011–2013) and warm years (2010, 2014–2016) in the California Current from daytime surface trawls for juvenile salmon (see Figure 23 for station locations). A total of 131 stations were included that had at least one sampling during both environmental regimes. Shown at bottom is the mean catch of a given species in the different conditions along with the results of a paired *t*-test comparing the catches from the two regimes.

fishes (Rice et al. 2012), and in the species composition of jellyfish assemblages (Reum et al. 2009). Based on trawl surveys in inlets inside Puget Sound in June and September 2007, Reum et al. (2009) determined that three species of Scyphomedusae (*Phacellophora camtschatica*, *Cyanea capillata* and *Aurelia labiata*) and one species of Hydromedusae (*Aequorea* spp.) were the most common species caught in these waters. The biomass of all species decreased seasonally between June and September and showed much variability among the four sampling areas. Rice et al. (2012) sampled a broader region of Puget Sound using pelagic trawls from May to August of 2003. Jellyfish from these surveys were not identified to species level but were combined as jellyfish biomass to compare with various fish species that were caught. However, these authors noted that the above species tended to dominate the catch along with the smaller hydrozoans and ctenophores. Jellyfish biomass was highest in the southern part of the sound, often exceeding 80% of the total biomass of the catch, but this decreased substantially to the north. Monthly changes were also observed and related to the changing physical environment in the area throughout the summer. In a recent study, Greene et al. (2015) analysed longer-term patterns of biomass of jellyfish using the above studies and comparing it to earlier work done in the 1970s and 1980s. They found that the proportion of hauls with large jellyfish catches have increased over this period in all three sub-basins examined, and these were related to increases in anthropogenic stressors, although negatively related to total forage fish biomass. These patterns suggest significant differences in the structure of pelagic foodwebs within Puget Sound that could have important management implications.

Substantially less is known about the vertical distributions of large medusae in the California Current, although recent efforts on tagging suggest that *Chrysaora fuscescens* performs stereotypical vertical excursions (Fannjiang et al. 2019). Based on a comparison of tows made in the upper 18 m to simultaneous tows made from 20 to 40 m during daytime in the California Current, Suchman et al.

(2012) found no significant difference in the density of either *Chrysaora fuscescens* or *Aequorea* spp. Brodeur et al. (2019) conducted tows at three depths during nighttime at two stations along the northern Oregon coast. Neither station showed a definitive pattern in the vertical distribution of *Aequorea* spp. with one station showing the highest abundance in the shallowest tow (upper 20 m) and another showing the highest at the deepest tow (around 50 m). However, both these studies were done without closing nets, so there is likely to be some contamination from the shallow layers in the deeper nets. Utilising a ROV, a total of 771 *Chrysaora fuscescens* were counted (from 24 dives) between the surface and the seabed, over bottom depths ranging from 20 to 40 m off central Oregon between June and September 2008. Approximately 77% of jellyfish were observed in the upper 20 m, although the mean depth of abundance varied among stations (Figure 27).

Space – time Densities of the two dominant larger medusa species in the northern California Current, *Chrysaora fuscescens* and *Aequorea* spp., have been monitored as part of a surface trawl survey in the northern California Current conducted every June and September from 1999 to 2012 (Suchman et al. 2012, Morgan et al. 2019). With few exceptions, *Chrysaora fuscescens* dominated the catch and was generally one to two orders of magnitude higher than that of *Aequorea* (Figure 28).

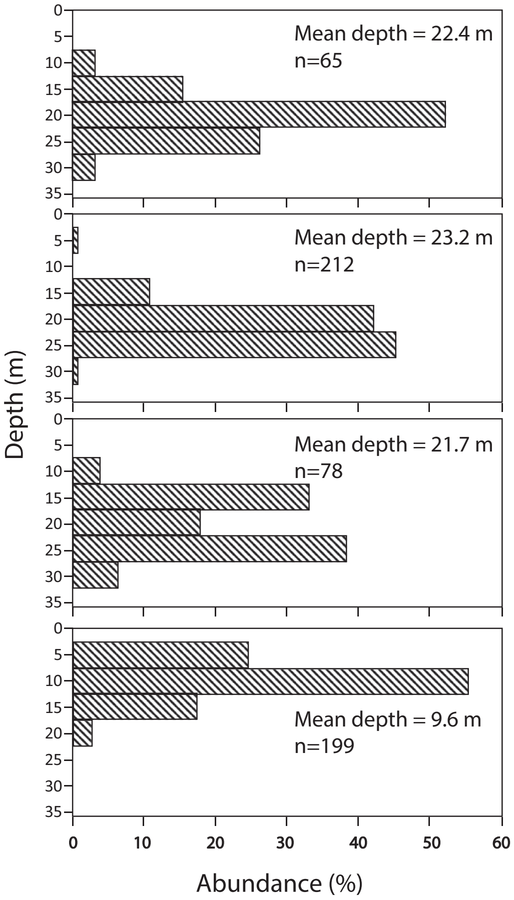

Figure 27 Daytime vertical distribution of *Chrysaora fuscescens* off Oregon (45.0°N, 124.3°W) based on four deployments of a ROV by the Oregon Department of Fisheries and Wildlife (ODFW) on September 16, 2008 (Data courtesy of D. Fox, ODFW). Shown in the upper right corner are the proportions of the total found at each 5 m depth interval with the mean depth (m) and number of individuals observed during each deployment.

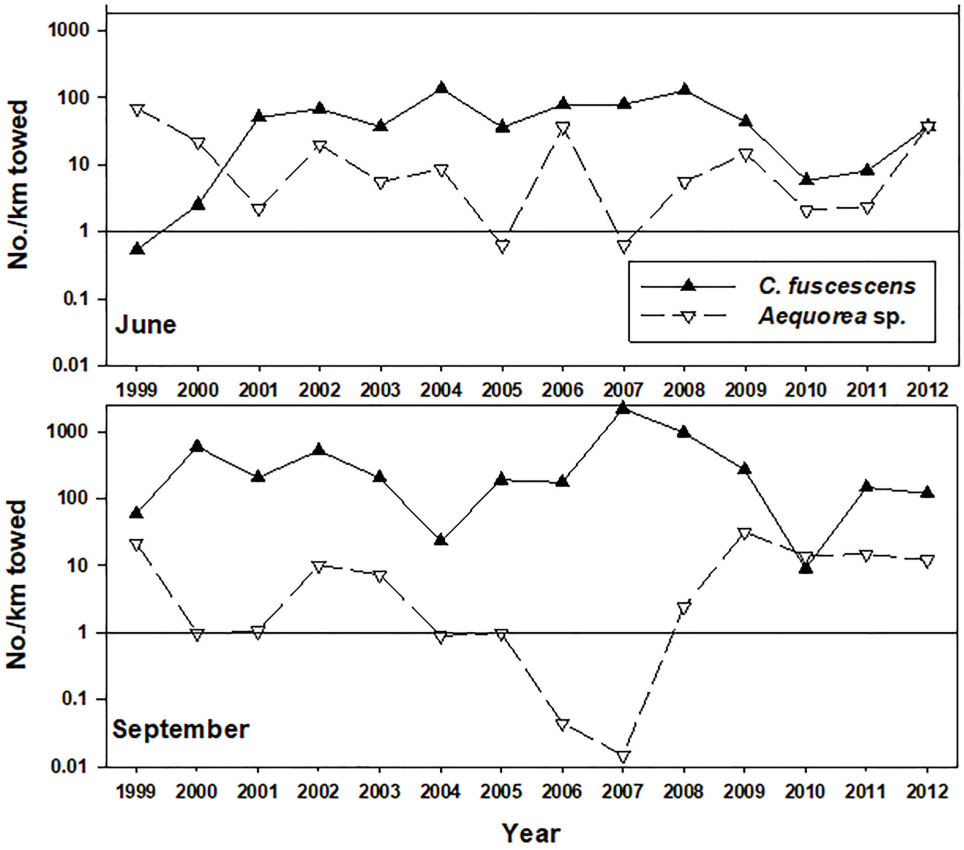

Figure 28 Catches of *Chrysaora fuscescens* and *Aequorea* spp. in annual surface trawl surveys off Washington and Oregon in June (upper panel) and September (lower panel) from 1999 to 2012.

Catches of both species returned to a more typical level in June 2012, following below-average catches for 2010 and 2011, possibly due to the lingering effects of the 2010 El Niño (Figure 28). In September 2012, catches of both species were similar to those seen in 2011, with densities of *Chrysaora fuscescens* being approximately an order of magnitude higher than those of *Aequorea*, similar to that seen in earlier years by Suchman et al. (2012). Morgan et al. (2019) analysed 20 years (1998–2017) of June surface trawl catch data and showed that the last few years were the most anomalous in jellyfish catches, with *Aequorea* spp. exhibiting densities two standard deviations (SD) above the long-term mean in 2015 and 2016, whereas *Chrysaora fuscescens* was one SD below the mean for these two years. The recent increase in *Aequorea* was attributed to relaxed upwelling and onshore transport associated with the large marine heatwave that occurred during those two summers (Di Lorenzo & Mantua 2016, Peterson et al. 2017).

Sorenson (2018) examined in detail the time series of the abundance of *Aequorea* to 18 years (1999–2017) and showed it was highly variable interannually, seasonally and across stations. The highest abundances were recorded in 2015 and 2016, reaching more than 16,000 km^{-2} at some locations. Using generalized additive models of *Aequorea* abundance and distribution related to environmental variables, Sorenson (2018) showed a close relationship of these with *in situ* environmental conditions, with a positive correlation to both SST and salinity. Larger-scale environmental drivers including the Pacific Decadal Oscillation (PDO), discharge from the Columbia River and upwelling strength also influenced *Aequorea* abundance.

Another long-term dataset involves the by-catch of gelatinous zooplankton (mostly large medusae) in triennial bottom trawl surveys conducted by the Alaska Fisheries Science Centre, NOAA from 1980 to 1992 (data provided by M. Wilkins, Alaska Fisheries Science Center, NOAA) that extend from northern Washington to Southern California. Catches were highly variable but showed low jellyfish abundance during the El Niño events of 1983 and 1998, similar to those seen in other studies covered here, but also in 1986.

With respect to temporal trends in abundance in the southern California Current, the mean log-transformed catch of *Chrysaora fuscescens* and *Aurelia labiata* for the core survey area between 1990 and 2019 (excluding the years 2002–2004, for which data were not collected) was examined. This index is useful as a relative abundance time series, although developing an absolute abundance index is difficult given the uncertainty regarding net selectivity and the real or likely depth stratification of jellyfish, which are probably present at greater densities in the upper 20 m of the water column relative to the typically 30–40 m depths targeted in this survey. Note that a key assumption made in the development of this index is that "problem hauls", in which the nets are either damaged or "blown out" due to an extremely high (but subsequently un-quantified) abundance of jellyfish, or in which hauls were aborted due to the high presence of jellyfish in the water (in such cases, an approximate species composition is estimated visually), have the estimated catch rate set to that of the highest observed abundance in good performance hauls. Despite these limitations, the two species show dramatic interannual variations in abundance (Figure 29). During some periods, the abundance of these two species appears to be inversely related, while in some years (especially 2018 when both species reached peak abundance), they coincide (Figure 29).

The temporal trends observed in these indices suggest both high interannual variability (consistent with high interannual variability observed in many of the time series of micronekton documented in this survey), and no clear indication of either a monotonic increase or decline in jellyfish abundance in this region over time. In general, years of greatest jellyfish abundance tended to be relatively cool, high transport years that also favour increased abundance of young-of-year groundfish, krill and market squid (*Doryteuthis opalescens*), while during warm, less productive years (such as the 1998 El Niño year and the unusually low productivity period between 2005 and 2006), jellyfish abundance declines considerably (unpublished data; J. Field). Off California, the temporal trends of midwater Hydromedusae have been related to major climate forcing such as El Niños (Raskoff 2001).

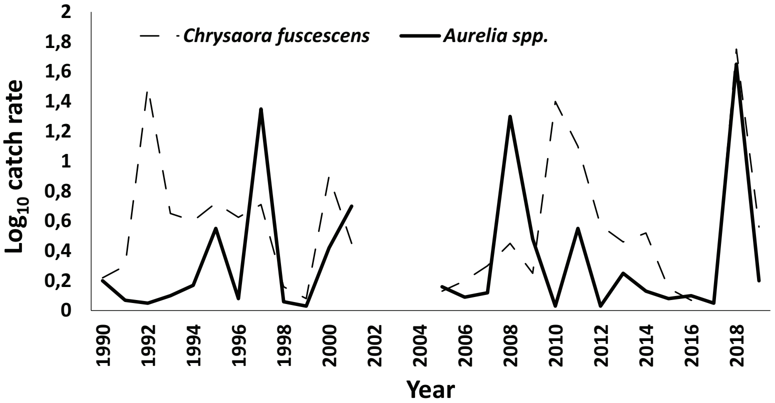

Figure 29 The mean of the log-transformed catch rate for the two most frequently occurring scyphozoan species encountered in the Southwest Fisheries Science Center midwater trawl survey conducted off Central California, 1990–2019 (no data available for 2002–2004).

Biomass, growth and mortality

Biomass The length–mass relationships for *Chrysaora fuscescens* and *Aurelia labiata* are shown in Supplementary Table 1A. With respect to absolute abundance, some work has been done to develop estimates of jellyfish abundance in the California Current region using acoustic backscatter from which estimates of abundance by area were developed for the Monterey Bay and Gulf of Farallones regions (Graham et al. 2010), with mean densities estimated to be on the order of a quarter of a million jellyfish within a square mile of ocean habitat. Ultimately, some combination of net sampling and acoustics could lead to greatly improved estimates of abundance, distribution and year-to-year variation in large Scyphomedusae in this region.

Growth, mortality and longevity Spatial variations in the mean and variation in size of the dominant macromedusae were evident in the coastwide rockfish surveys based on the regions shown in Figure 24. Both *Chrysaora fuscescens* and *Aurelia labiata* showed their largest sizes and greater variability in bell diameters off central California compared to the northern California Current (Figure 30). There was relatively little interannual variation in the bell diameter sizes for *Aequorea* spp. in the northern California Current, although the sizes during the warm year of 2017 was substantially lower than the other years (Figure 30).

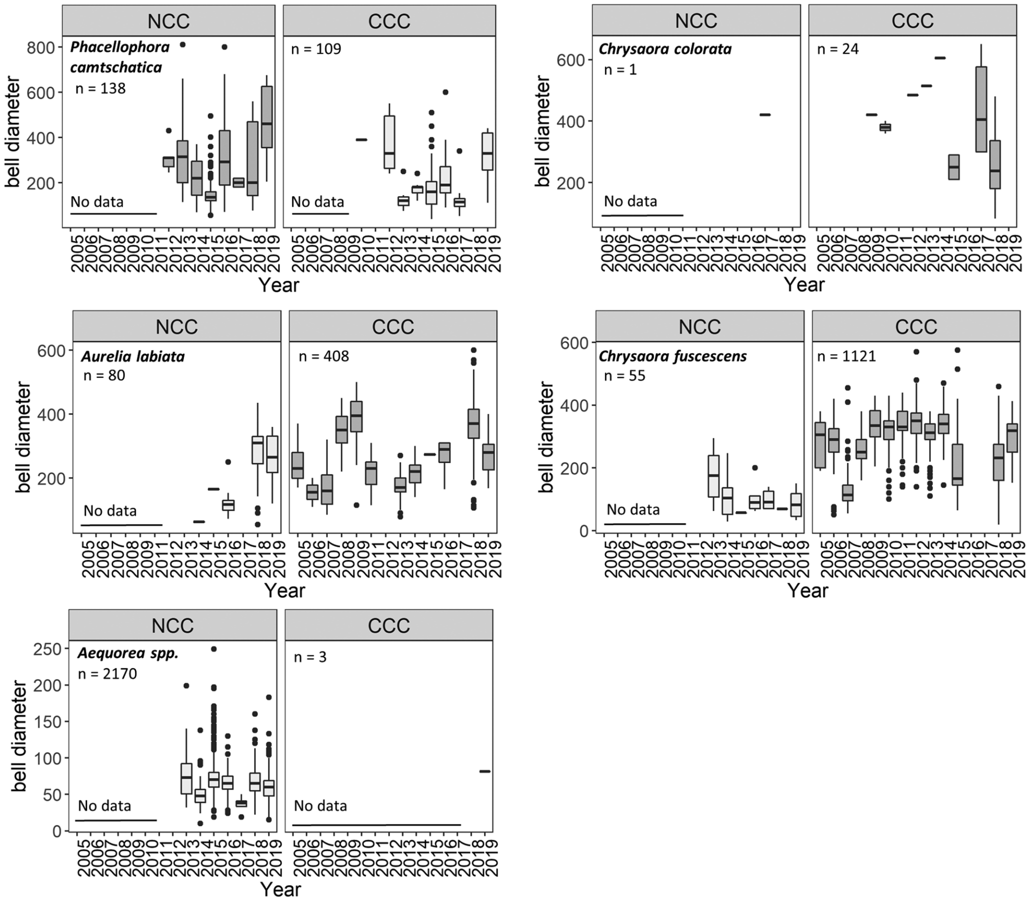

Figure 30 Spatial variation in bell diameters (mm) of the dominant species by year and geographical area. See Figure 23 for extent of the geographical regions (NCC northern California Current, CCC Central California Current). Total number of measurements (*n*) is given for each species.

The first study to examine seasonal growth patterns of Scyphomedusae in the California Current was that of Shenker (1984). Based on changes in umbrella diameter, *Chrysaora fuscescens* grew rapidly in the summer months from a mean size of 8.6 cm in May to 18.5 cm in August. Using monthly data collections described in Suchman et al. (2012) from April to October (Figure 31), it was noted that *Chrysaora fuscescens* increased in bell diameter from May through August, but

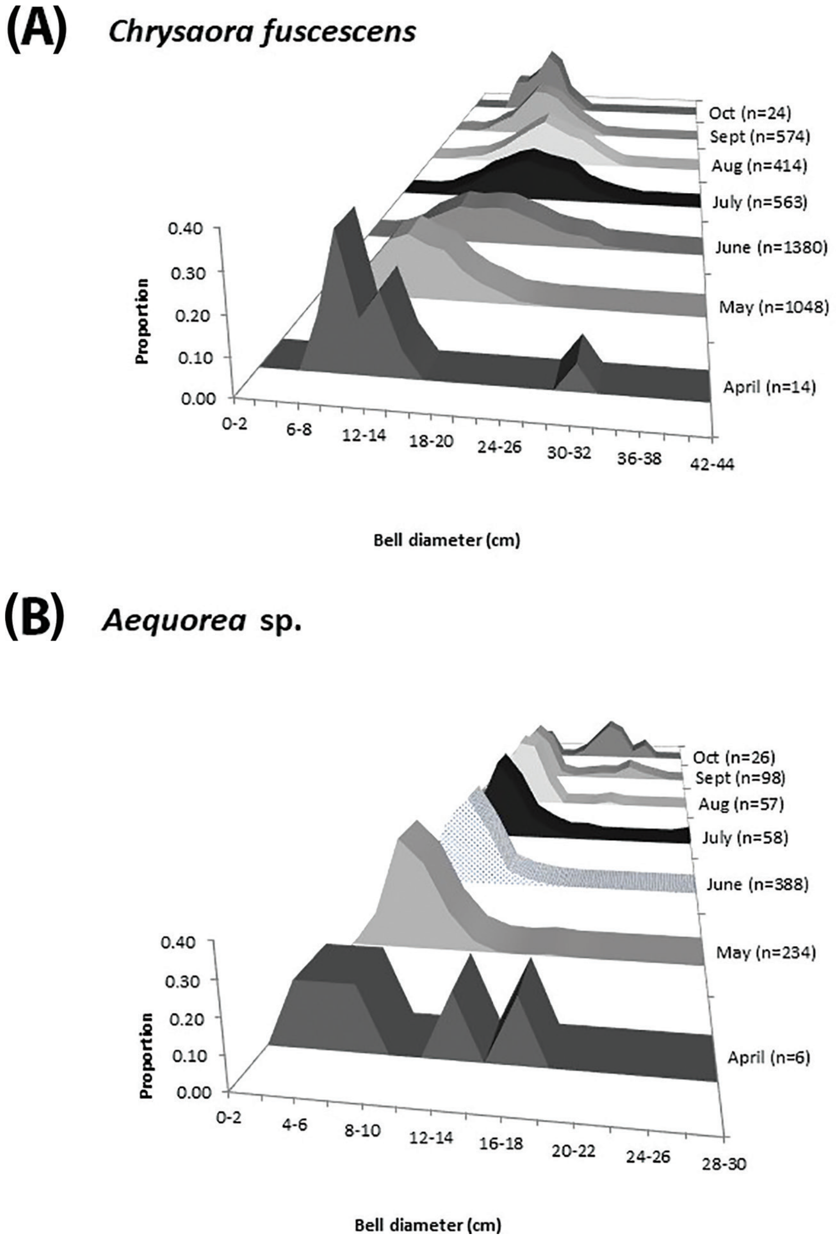

Figure 31 Bell diameter frequency for *Chrysaora fuscescens* (A) and *Aequorea* spp. (B) by month from surface trawl collections off Oregon and Washington from 2001 to 2009. All collections were made from off the Columbia River, Oregon to Grays Harbor, Washington. The sample size for each month is given in parentheses.

subsequently decreased in September and October. Whether this reflects natural senescence, shrinkage due to less food available or a preferential mortality of the larger individuals in the population is not known. Potentially because of different life histories, *Aequorea* spp. shows a more bimodal size distribution pattern with a moderate increase in the main smaller mode but with a second mode appearing in late summer and even persisting until April (Figure 31). This pattern is not likely to be caused by increased growth during this brief period, but instead these larger individuals likely correspond to the larger offshore species (*Aequorea coerulescens*) occurring in this region (Mills and Rees 2007) that may be advected into coastal waters when the seasonal upwelling subsides. There were two survey years when winter samples along with other seasonal data were taken: 2003 when May, June, September and November had surveys, and 2018 when March, May and June were sampled. While *Chrysaora fuscescens* showed significant declines in bell diameter by November 2003, compared to June and September (Kolmogorov–Smirnov; $p < 0.001$; Figure 32A), the *Aequorea* spp. almost doubled in size in November relative to the other months in the year (Figure 32B) possibly indicating that two species were present. In March 2018, *Chrysaora fuscescens* was of a similar size in March and May (Figure 32C), while *Aequorea* in March were again almost double the size of the May and June period, although with low sample size, showing large winter bell diameters (Figure 32D).

As a measure of growth, the change between the average bell diameters of *Chrysaora fuscescens* between May and June (2001–2019; 15 years of survey) and *Aequorea* (11 years of survey) was

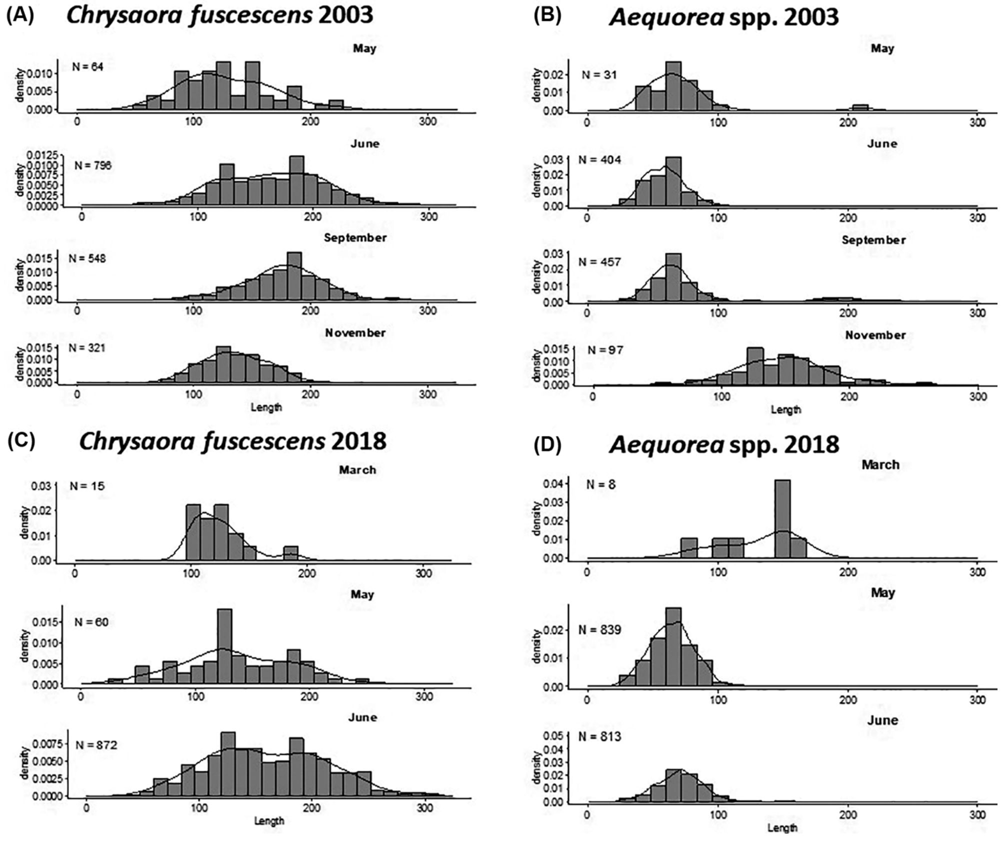

Figure 32 Bell diameter (mm) density plots of *Chrysaora fuscescens* (A and C), and *Aequorea* spp. (B and D) by month (May, June, September and November) in 2003, and March, May and June 2018. The number of measurements is shown in the upper left of each plot.

estimated and related to ocean conditions as measured by winter PDO (Figure 33). The growth of *Chrysaora fuscescens* and *Aequorea* between May and June was significantly higher during more negative, or colder, winter conditions (Figure 33). Using the same time series, years were divided into cold or warm regime based on the rank of the means from the ocean ecosystem indicator table provided by NOAA Fisheries ocean ecosystem indicator data.[4] In May, the size of *Chrysaora fuscescens* was significantly larger during warmer ocean condition (Kolmogorov–Smirnov; p <0.001; Figure 34A), suggesting faster spring growth, yet by June, *Chrysaora fuscescens* were significantly larger in cold ocean conditions (Kolmogorov–Smirnov; p <0.001; Figure 34A) suggesting faster summer growth of the population. For *Aequorea*, there were not significant size differences between May ocean conditions (Figure 34B), nor between May and June during warm ocean conditions, but there was a significant increase in size between May and June during cold ocean conditions (Kolmogorov–Smirnov; p <0.001; Figure 34B).

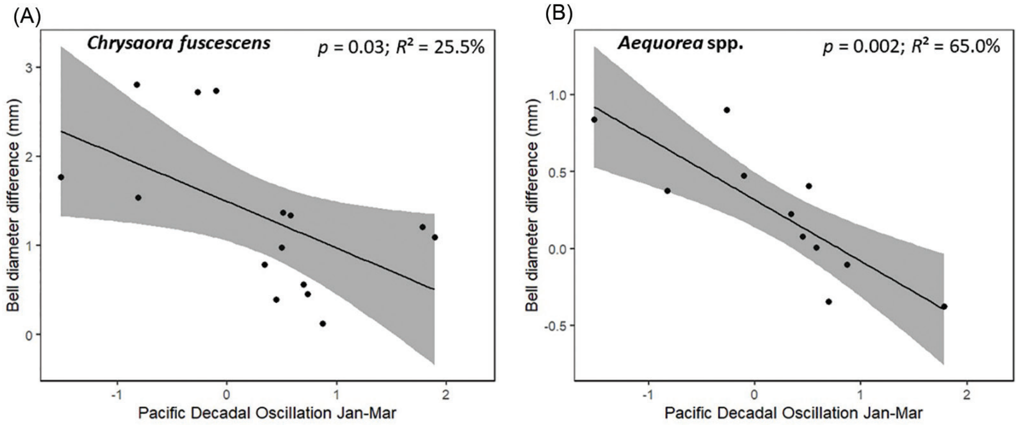

Figure 33 Relationships between the difference in average bell diameter (mm) between (A) *Chrysaora fuscescens* and (B) *Aquorea* spp. caught in May and June for each survey year to the January–March PDO. The relationships between the January–March PDO and the difference in average bell diameter (mm) of jellyfish caught in May and June each survey year for (A) *Chrysaora fuscescens* and (B) *Aquorea* spp.

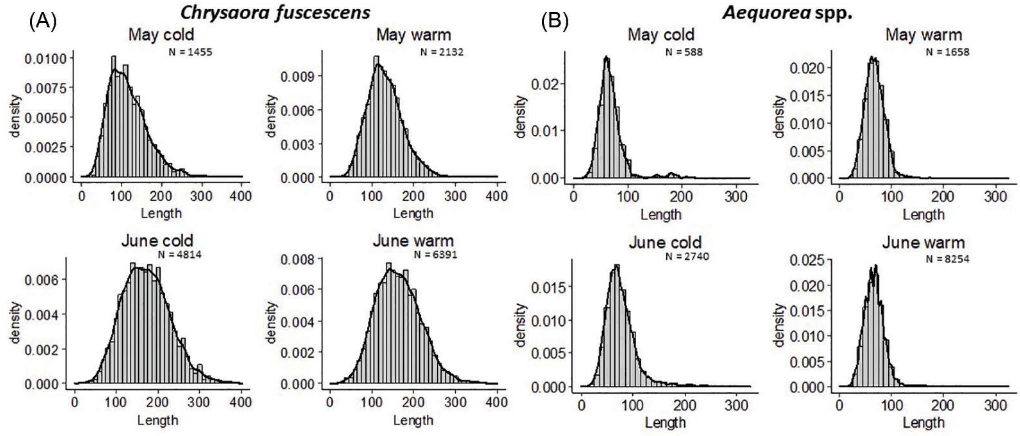

Figure 34 Bell diameter (mm) density plots of *Chrysaora fuscescens* (A) and *Aequorea* spp. (B) by month (May or June) relative to ocean conditions (cold or warm). The number of measurements N is shown in the upper right of each plot.

There are scant field data on the longevity of macromedusae in the NE Pacific Ocean. Albert (2005) studied a population of *Aurelia labiata* in an enclosed bay in British Columbia and found that medusae there generally lived for more than one year and that up to 40% of the adult medusae may be two years of age or older. The question of how long jellyfish can exist as medusae has been evaluated in the laboratory setting, as both *Chrysaora fuscescens* and *Aurelia labiata* have been maintained in aquaria for many years (Raskoff 2003), showing that they have the potential to at least overwinter in the ocean. Hydromedusae, on the other hand, live a relatively short time even in captivity (three to six months; Raskoff 2003), and individuals within a given cohort will tend to all die within a short period of each other.

Reproduction

Sexual The life histories of these (and other) species have been rigorously evaluated by a combination of field and aquarium studies (e.g. Raskoff 2003, Widmer 2005, 2006, 2008b). All Scyphomedusae and the one Hydromedusa included here are known to have separate sexes, with some having distinctive differences in gamete colour between the males and females. *Aurelia labiata* and *Cyanea capillata* are known to brood their planulae, with the males developing sperm follicles that are captured by the females and moved towards their gastric pouches that are lined with eggs (Arai 1997). Mature planulae are then released into the environment for transformation and settlement of the sessile phase. The remaining medusae are broadcast spawners and shed gametes into the water column, especially when in aggregations, and the drifting fertilized eggs then develop into planula larvae and settle to form scyphistomae (polyps) in the case of the Scyphomedusae, and gonozooids for reproduction in the case of the Hydromedusae. Cnidaria that are planula brooders may have less gene flow among populations (Hellberg 1996).

The seasonality of maturity and reproduction of jellyfish in the California Current is also a little-studied topic. The jellyfish *Aequorea* spp., *Chrysaora fuscescens* and *Aurelia labiata* have conspicuous gonads when sexually mature and ripe individuals have been consistently observed in the May, June and September surveys done in the northern California Current (E. Daly, unpublished data). In the California Current, mature *Chrysaora fuscescens* males and females were collected in January (Widmer 2008b), and also mature *Aurelia labiata* were collected February-May (Widmer 2005). At the most northern area of the northern California Current off the west coast of Canada, female *Aurelia labiata* have been shown to be carrying mature planula larvae in November, and as such, males were most likely mature in September or October (Albert 2005).

Asexual Very little is known about the benthic or early larval stages of medusae in the California Current. During an underwater survey of hard structures in Yaquina Bay, Oregon, Heitstuman (1994) found only a few occurrences of the polyps of *Aurelia labiata*, mostly on undersides of man-made structures (jetties and piers), and no *Chrysaora fuscescens* polyps were found despite extensive searching. Conley (2013) used molecular techniques to identify the scyphistomae of medusae in Coos Bay in Southern Oregon and the specimens that were sequenced were all identified as *Aurelia labiata*. The location of the benthic polyp stage for the larger medusae of the California Current continues to remain a mystery in the field. While *Aurelia labiata* polyps have been identified in several small bays of the Oregon coast and polyps may also be found on rocky reef areas further offshore, the adult medusae are generally oceanic.

Strobilation of *Aurelia labiata* polyps in Puget Sound occurred in January and February, when light, temperature and salinity were at the lowest recorded levels in the year (Purcell et al. 2009). In the California Current, strobilation of *Aurelia labiata* occurred in February–April (Galigher 1925, Widmer 2005). The timing and production of the sessile stage, as well as timing of strobilation, have been investigated in the laboratory for *Chrysaora fuscescens* in the California Current (Widmer 2008b). Mature adults were collected in January, and gametes were obtained; polyps were fully developed by 50 days post-spawning. By day 231, a single polyp had formed 51 polyps and 53 podocysts. The polyps began strobilation at 286 days post-spawning, and up to 60 ephyrae were produced per polyp (Widmer 2008b). Production of gametes by the Hydromedusa *Aequorea victoria* was measured at 300–8600 eggs day^{-1} medusa^{-1}, daily for seven days (Larson 1986). Changes in temperature, light levels, salinity and pH have all been shown to affect the return of the sessile stage to the pelagic medusa (Raskoff et al. 2003). The temperature range to maintain successful sessile states of California Current jellyfish of our study region ranged primarily between 10 and 15°C (Raskoff et al. 2003, Widmer 2005, Purcell et al. 2009, Treible & Condon 2019). The scyphozoan medusae of our study are all polydiscus – with many ephyrae being release per strobilation event (Purcell et al. 2009, Helm 2018), and the colony of *Aequorea victoria* hydroids produces many medusae (Larson 1986).

High survival and settlements of polyps, strong production of ephyrae and positive advection of medusae into coastal waters can create scenarios where high biomasses of jellyfish medusa can bloom (Moloney et al. 2010). Location of the ephyrae can potentially aid in the identification of where in the ocean the polyp phase is located, especially through the use of circulation models (Johnson et al. 2001, Barz et al. 2006). Key to this is the identification of ephyrae to species from plankton samples, which is not being done at present. Spawning of adult medusae in the laboratory and careful description of the ephyrae can allow us to use plankton samples to understand more fully the population dynamics of medusae in the California Current (Widmer 2006, 2008b).

Interactions with other species and human activities

Diet

There has been a limited number of gelatinous zooplankton diet studies from the California Current. Graham (1994) reported that preys of *Chrysaora fuscescens* in Monterey Bay included doliolids and siphonophores, which are often highly abundant in the same frontal region as jellyfish swarms. Suchman et al. (2008) analysed the diets of *Chrysaora fuscescens*, *Phacellophora camtschatica* and *Aurelia labiata* in relation to available plankton from specimens collected in August 2002. These authors found that euphausiid eggs, calanoid copepods, cladocerans and other gelatinous taxa were particularly important in their diets. Based on diet and laboratory measurements, these authors suggested that *Chrysaora fuscescens* had the potential to remove between 10% and 12% of the overall standing stocks of these preys per day and considered that jellyfish may be especially important predators on euphasiid eggs and copepods in nearshore waters (Suchman et al. 2008). More recent work on *Chrysaora fuscescens* conducted in June, July and September of 2014 shows that certain prey types are more vulnerable to predation by jellyfish (Zeman et al. 2016). Gut content analysis of the medusae showed positive prey selection for vulnerable, slow-moving taxa, (e.g. fish and invertebrate eggs and appendicularians). Predation on ichthyoplankton was particularly high in June when medusae are growing rapidly and when fish eggs, particularly those of northern anchovy *Engraulis mordax*, were abundant in the plankton. Copepods, though abundant in the plankton, were negatively selected relative to their availability (Zeman et al. 2016). Experiments in laboratory kreisels have shown that *Chrysaora fuscescens* have high clearance rates on *Artemia* prey and that these feeding rates are not affected by current speeds (Zeman 2015).

Several studies have used the stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to examine trophic position and niche width of jellyfishes in this region. Miller et al. (2008) and Brodeur et al. (2008b) have used $\delta^{15}N$ to examine the relative trophic level of several common jellyfish species in the Northern California Current, comparing these to the dominant small pelagic forage species. They found that *Chrysaora fuscescens* and *Aurelia labiata* occupied about the same trophic level and were only slightly lower than such important forage fishes as Pacific herring (*Clupea pallasii*), Pacific saury (*Cololabis saira*), northern anchovy and Pacific sardines. Based on whole-body $\delta^{13}C$ values, *Chrysaora fuscescens* showed the most inshore distribution, while *Aequorea* spp., *Phacellophora camtschatica* and *Aurelia labiata* had similar isotope values indicative of more offshore distribution and feeding (Supplementary Table 4, Miller et al. 2008). A similar study conducted by Naman et al. (2016) in Puget Sound showed that although there were high overlaps in isotope ratios between the jellyfish species examined and forage fishes, jellyfish were often more enriched in ^{13}C and depleted in ^{15}N than fish, which may indicate a more marine-influenced diet. However, jellyfish were found to have narrower trophic niches than fishes, and these were less associated with physical and biological variables measured (Naman et al. 2016).

Parasitism

There are few direct observational studies of the associations of hyperiids with macromedusae in the California Current, although the most abundant hyperiids such as *Hyperia medusarum* and *Hyperoche medusarum* are often observed living within the bells of several medusan hosts in dip-netted specimens (Daly and Brodeur, personal observations). In Puget Sound, Towanda and Theusen (2006) found an increase in parasitism of *Hyperia medusarum* in the oral arms of *Phacellophora camtschatica* through the summer reaching 100% of the examined hosts by autumn with a maximum of 446 amphipods on a single medusae. Other crustaceans, such as larval crabs, are ectoparasitic on this same host species (maximum 336 larvae per individual), consuming parts of their host during development (Towanda & Theusen 2006).

Predation

When prevalent, gelatinous zooplankton may provide an alternate pathway for energy flow that can lead to production in higher trophic levels. Although Scyphomedusae can grow and feed at high rates, their bodies are composed mostly of water and thus are not typically a good food source for larger pelagic organisms. With the notable exception of the large ocean sunfish (*Mola mola*) that specialise in large medusae prey, most marine fishes do not consume large Scyphomedusae prey. Only a few fish species in the California Current are suspected to be selective feeders upon medusae, including prowfish (*Zaprora silenus*), and medusafish (*Icichthys lockingtoni*) and their relatives, which are often commensal with medusae as juveniles. Several species of rockfishes are known predators of a wide range of gelatinous plankton, particularly thaliaceans, but they also eat a broad range of cnidarians, ctenophores and other gelatinous macro-zooplankton (Adams 1987) particularly during low productivity years (Lee & Sampson 2009). Laidig et al. (1997) also noted that sablefish (*Anoplopoma fimbria*) caught in California waters preyed on both salps and gelatinous zooplankton, although neither constituted a substantial fraction of the total prey biomass. Brodeur et al. (2021) analysed the diets of many commercially important groundfishes in the northern California Current and found several species of rockfish were consumers of medusae, but they generally made up a small proportion of the diet.

Scyphozoans are also critically important prey for endangered Pacific leatherback sea turtles (*Dermochelys coriacea*), of which a significant fraction of the population migrates into the California Current during late summer and autumn to feed. Substantial fisheries management measures, including large area closures, have been implemented to protect sea turtles from fisheries impacts (particularly from the drift-gillnet fishery for swordfish and other highly migratory species). The spatial extent of the closures has been based on both survey data of turtle abundance and distribution, and telemetry data that indicate areas in which turtles engage heavily in foraging behaviour (Benson et al. 2007, 2011, Bailey et al. 2012). Individual turtles may eat 20%–30% of their body weight per day, and up to 1000 t per individual per lifetime, with the total Pacific-wide consumption by turtles estimated to be on the order of two million t per year (Jones et al. 2012). Consequently, a better understanding of the environmental drivers of scyphozoan abundance, population dynamics and distribution could help inform management measures taken to minimise fishing-related mortality on these critically endangered species.

There are likely to be few, non-parasitic invertebrate predators on the adult stages of living macromedusae, although some large medusae (e.g. *Phacellophora camtschatica*) are known to feed extensively on other adult medusae (medusivorous) in the California Current (Suchman et al. 2008). Although other jellyfish species are also known to be medusivorous, including *Chrysaora fuscescens*, *Aurelia labiata* and *Aequorea* spp., these are likely to eat mainly the younger stages of macromedusae, or other small gelatinous taxa such as ctenophores and salps (Suchman et al. 2008).

Associations with fish

As noted above, in the retention areas north and south of Point Reyes, there is a significant overlap in the distributions of *Chrysaora fuscescens*, the krill *Thysanoessa spinifera*, and those of juvenile salmon. This spatial overlap suggests that there may be potential competition between jellyfish and other animals that feed on zooplankton, such as forage fishes as suggested in the northern California Current (Brodeur et al. 2008b, 2014, Suchman et al. 2008). Brodeur et al. (2008b) examined the spatial overlap of the dominant jellyfish with important pelagic fish species in the Northern California Current. They found several fish species (particularly juvenile salmon and smelt) had relatively high overlap with *Chrysaora fuscescens* and to a lesser extent *Aurelia labiata* off southern Oregon (Brodeur et al. 2008b). Using a longer (13-year) time series of catches of *Chrysaora fuscescens* and catches of herring, anchovy and sardines, Brodeur et al. (2014) showed that the spatial patterns of the centroids of abundance and spatial overlap were highly variable during June and September. The three forage species showed inverse relations of abundance to the jellyfish abundance in both months. Finally, Ruzicka et al. (2016) showed that juvenile salmon had a high spatial overlap with *Chrysaora fuscescens* and they also showed inverse relationships of salmon survival to jellyfish biomass. These authors also noted that the feeding success of juvenile salmon in hauls with large numbers of jellyfish was lower than those caught in trawls with little or no jellyfish, implying that there was a negative impact of jellyfish on salmon possibly due to competition for food resources (Ruzicka et al. 2016).

Fisheries and human activities

The impacts of jellyfish blooms on humans are manifold, but the primary effects relate to those concerned with tourism (beach closures), power plant closures (clogging of intake systems), and both direct and indirect impacts on fisheries (Purcell et al. 2007, Graham et al. 2014). Unlike many systems at a similar latitude, the cool nearshore waters of the California Current are not conducive to the species of jellyfish that sting, much less kill, bathers, so they are generally not an issue for tourism here (Graham et al. 2014). Although blooms are known to clog intake systems of nuclear power plants in California, these have been attributed to salps and not medusae (Graham et al. 2014). However, large blooms of medusae can have major indirect effects on fish recruitment through consumption of early life stages (Purcell 1989, Zeman et al. 2016) and potential growth and survival of juvenile and adult fishes through shared use of food resources (Brodeur et al. 2008b). Due to the immensity and spatial variability of the California Current, these indirect effects are difficult to quantify and can only be approximated using models but are most likely to impact fish abundance and catch in years with major medusae blooms.

The direct economic impact of jellyfish upon commercial fisheries was studied by mail surveys sent to local fishers (Conley and Sutherland 2015) in the Northern California Current system off Oregon, where *Chrysaora fuscescens* is densely distributed (Suchman & Brodeur 2005, Brodeur et al. 2008b). Of the total respondents, 67% reported that jellyfish reduced their seasonal revenue, and the estimated economic impact of jellyfish on salmon and pink shrimp fishers was over USD650,000 during the peak jellyfish season in 2012. According to fishers' reports, the jellyfish impact is not solely upon net fisheries, but also upon hook and line fisheries. The spatial distribution patterns of the impacts on the salmon trolling fishing industry corresponded to the spatial distributions of *Chrysaora fuscescens* observed in large-scale research surveys (Conley & Sutherland 2015). Finally, as mentioned previously, extensive blooms of jellyfish can hamper surveys of fish populations by the scientific community, impacting and in some case preventing sampling in research surveys, leading to incomplete information on fish stocks, especially for pelagic species.

Macromedusae in ecosystem models

Although there is a substantial number of detailed food web models available for many of the LMEs of the world, very few of them have explicitly included gelatinous zooplankton, and if they did, they were often aggregated into a single group (Pauly et al. 2009), which did not capture the diversity of predator–prey interactions in this taxonomically diverse assemblage. One of the first modelling studies to examine the interactions of large scyphozoan jellyfish in a coastal ecosystem was an examination of the impact large blooms have on the Oregon upwelling ecosystem (Ruzicka et al. 2007). Using mass-balanced ECOPATH models parameterized for the pelagic ecosystem from numerous field studies, Ruzicka et al. (2007) compared the seasonal food consumption of large jellyfishes (primarily *Chrysaora fuscescens*) to that of forage fishes and other major components of the ecosystem. This study found that jellyfish can be the major consumers of zooplankton during the late summer months and can exert substantial top-down effects on several zooplankton groups. During time of peak abundance (summer), jellyfish pass on only 2% of their biomass to higher trophic levels, whereas forage fishes pass along 17% of their biomass to higher levels.

The previous consumer demand-driven ECOPATH model was re-expressed as a producer-driven end-to-end model (Steele & Ruzicka 2011) where the ecosystem-wide consequences of changes in energy flow through key nodes in the food web could be evaluated. As an example, increasing the energy flow to jellyfish without increasing the overall productivity of the model led to a substantial decline in the productivity of forage fish in this system (Figure 35).

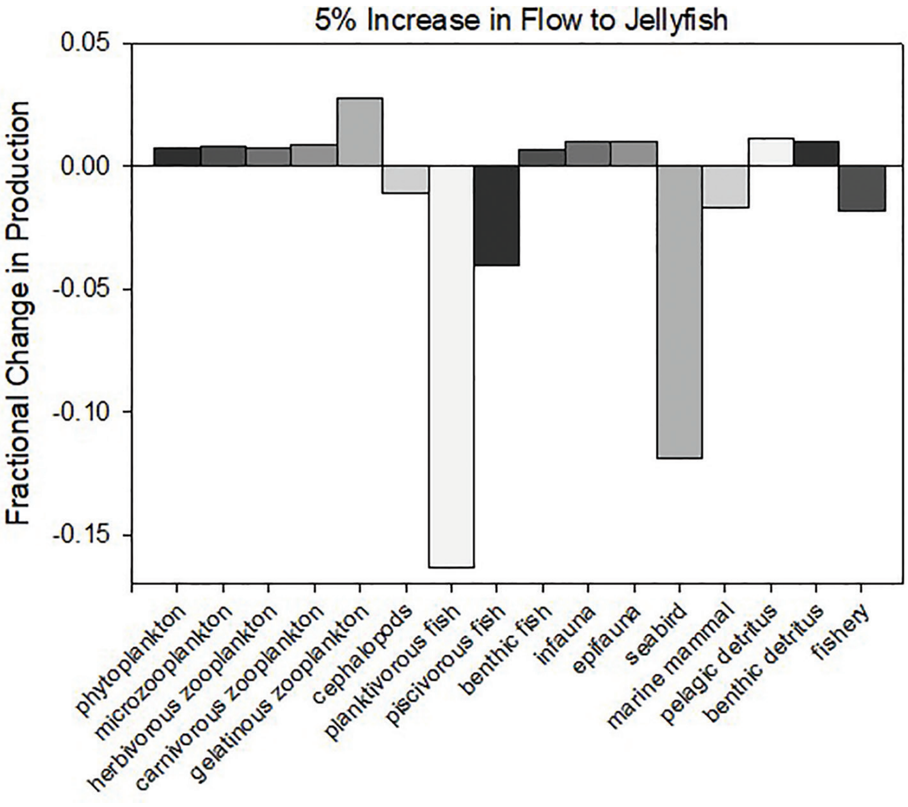

Figure 35 Output (fractional change in production of each trophic group) of a scenario from the re-expressed producer-driven end-to-end ECOPATH model where the amount of food going to jellyfish is increased by 5% compared to the base model, without any increase in the total productivity of the model (modified from Brodeur et al. 2011).

These end-to-end models have been extended to examine interannual variability in the relative roles that jellyfish, forage fish and euphausiids play in the Northern California Current driven by nutrient input rates (Ruzicka et al. 2012). These results indicate that jellyfish have a much greater footprint (the direct and indirect impact of a consumer on lower trophic levels) and smaller reach (the direct and indirect impact of a consumer on higher trophic levels) than forage fishes, and much less than euphausiids (Brodeur et al. 2011, Ruzicka et al. 2012). Jellyfish were thus a much less efficient energy transfer node in the foodweb than either other consumer groups. Additional work has compared the northern California Current to other North Pacific ecosystems including the Gulf of Alaska and eastern Bering Sea (Ruzicka et al. 2013, 2020, Robinson et al. 2014), and found that jellyfish are more important as consumers in the northern California Current than either of these other systems. Similarly, a lower trophic model that included a dominant scyphozoan jellyfish (*Chrysaora melanaster*) suggests the lower trophic Bering Sea ecosystem has little sensitivity to changes in jellyfish consumption (Gibson & Spitz 2011). However, the critical importance of *Chrysaora fuscescens* and other gelatinous prey to leatherback sea turtles, and potentially other select predators is a reminder that the role of jellyfish in food webs and to higher trophic-level groups should not be understated (Hetherington et al. 2019).

Canary Current ecosystem

Description

The Canary Current system is located along the NW coast of Africa from the Bissagos Islands in the South of Guinea-Bissau (around 11°N, 16°W) and Senegal to Morocco near the Strait of Gibraltar (around 36°N, 5°W), with a northern extension along Portugal and north-western Spain referred to as the Western Iberian Upwelling System. The whole system can be divided into two major domains associated with either the south-eastern boundary of the North Atlantic subtropical gyre (NASG) or the north-eastern North Atlantic tropical gyre (NATG) (Figure 36) (Pelegrí & Peña-Izquierdo 2015). The area is characterized by four waters masses: North Atlantic Central Water (NACW), North Atlantic Deep Water (NADW), Antarctic Intermediate Water (AAIW) and intermediate waters from the Mediterranean (MW) (Vélez-Belchí et al. 2015).

Three water masses are identifiable off Northwest Africa: South Atlantic Central Water (SACW), Eastern North Atlantic Central Water (ENACW) and Mediterranean Intermediate Water (MIW). In the upper water layer (0–500 m), the SACW and ENACW are dominant, with the well-oxygenated ENACW mixing with the salty sub-11°C MIW coming from the Strait of Gibraltar. A frontal zone is located off Cape Blanc at 21°N that separates the SACW and ENACW where mixing occurs. The ENACW has a salinity of ~36.7, whereas the SACW has a lower salinity maximum of 35.8 (Emery 2001), and off Mauritania the latter water has dissolved oxygen concentrations approaching 1 $mL{\cdot}L^{-1}$ (Glessmer et al. 2009).

Seasonality in the rhythm of the Azores anticyclone, the Saharan depression and the Intertropical Convergence Zone (ITCZ) determines the balance of the trade winds in the region and therefore the mode of circulation along the West African coast (Wooster et al. 1976, Parrish et al. 1983): it influences the average length of the upwelling season. Upwelling along the coast of northern and central Morocco occurs in summer (Wooster et al. 1976, Roy 1991, Makaoui et al. 2005) when wind stress there is greatest (Barton et al. 1998, Pelegrí et al. 2005), while off Mauritania and Senegal it occurs in winter. The Saharan Morocco enjoys permanent upwelling in two well-defined zones: between Cape Boujdor and Dakhla and the between Cape Barbas and Cape Blanc (Hughes & Barton 1974, Parrish et al. 1983).

The Cape Blanc region (20°50′N) is the southern limit of summer upwelling (Barton et al. 1998). It is considered as a mixing zone of two bodies of water of different origins, ENACW and

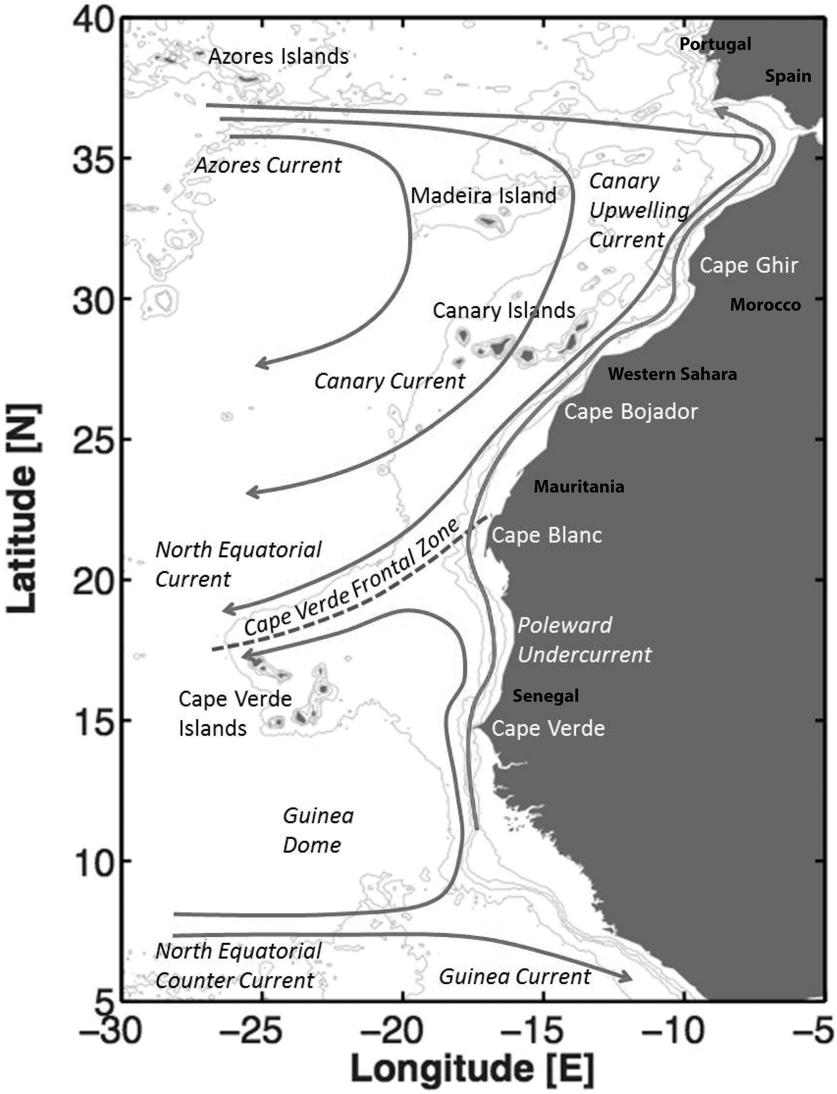

Figure 36 Map showing the key geographic features and oceanographic currents off NW Africa (Pelegrí & Peña-Izquierdo 2015).

SACW (Roy 1991). The shift of the SACW towards the north is observed up to a critical latitude of 23°N (Hagen 2001), which gives the zone between 21 and 23°N a particular-rich plankton (Binet 1991).

As would be expected, temperature at the surface and depths of 100 and 200 m shows winter and spring as the coldest seasons while summer and autumn are the warmest (Figure 37) (Benazzouz et al. 2014). According to Valdés & Déniz-González (2015), surface water temperatures in the region have increased by an average of 0.82°C per decade for the period 1982–2013.

The dynamics of plankton assemblages and populations following upwelling has been described in numerous works off NW Africa and, as in other EBC systems, the highest production is observed after the rise of deep water to the surface (Grall et al. 1982). In northern Morocco, where upwelling is seasonal, there is a significant lag between the development of phytoplankton and that of

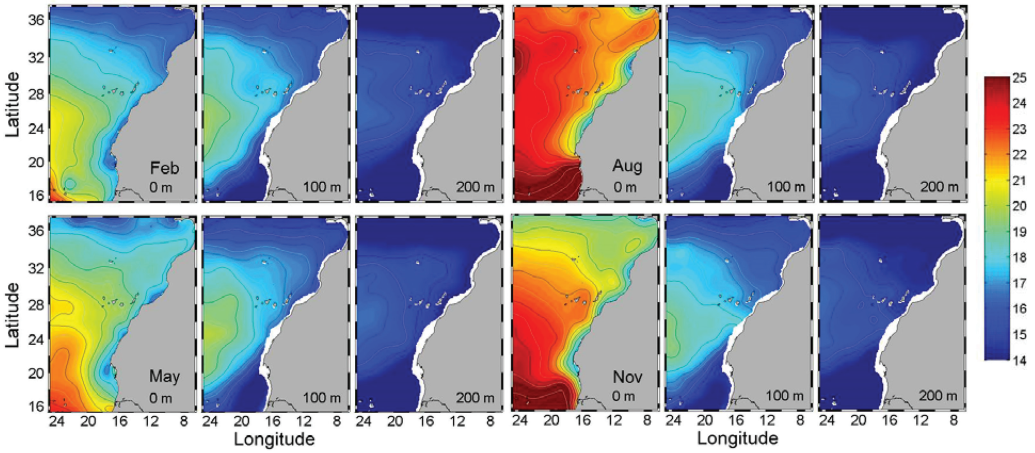

Figure 37 Seasonal changes in ocean temperature off NW Africa at sea surface, 100 and 200 m (Pelegrí & Benazzouz 2015).

zooplankton, which leads to a mismatch in productivity and a system imbalance (Furnestin 1957, 1976). Further south, where upwelling is permanent, the highest annual production rates are observed between Cape Barbas and Cape Blanc (Pelegrí & Peña-Izquierdo 2015). In this zone, phytoplankton blooms are observed on the fringes of the upwelling plume and zooplankton take maximum advantage of this downstream of the upwelling centre (Grall et al. 1974, Dupouy et al. 1986 in Binet 1991). Ecological transfer from phytoplankton to zooplankton is generally poor over the continental shelf owing to the temporal mismatch in response of primary and secondary producers (Binet 1991), although rapidly developing species, such as salps and cladocerans, can be abundant there (Le Borgne 1983).

North of 25°N, low concentrations of chlorophyll were observed offshore and high concentrations were noted near the coast (Auger et al. 2015) (Figure 38). In the south, however, high concentrations of chlorophyll extended well offshore (Figure 39). Based on the Intergovernmental Oceanographic Commission (IOC) Technical Series Report (Valdés & Déniz-Gónzález 2015), the chlorophyll concentration computed from SeaWIFS (1998–2003) shows a negative trend in the whole area, except for the area between Cape Blanc and northern Mauritania (Figure 39).

The Canary Current system is markedly heterogeneous, with a mosaic of mesoscale structures that reflect spatial and temporal variability often associated with the shape of the coast, bathymetry and local winds. Fronts, filaments and eddies play an important role in coupling physical and biological processes, exporting coastal water offshore (McGillicuddy et al. 1998) to increase primary production there. Surface eddies can modify circulation leading to a decrease in upwelling intensity McGillicuddy et al. 1998), whilst the relatively fine filamentary structures (Flament et al. 1985) that are often associated with capes (Marchesiello et al. 2003) can extend offshore over great distances to connect coastal upwelling with the open sea (Figure 39). These structures represent one of the permanent and dominant components of the dynamics of upwelling systems (Chavez et al. 1991), exporting nutrients (Jones et al. 1991), chlorophyll and zooplankton to the open sea, and their distinctive temperature and chlorophyll signals can be observed by satellite (Benazzouz et al. 2014). Two near-permanent filaments are located at Cape Ghir (30°38′N) and Cape Blanc (21°N), while other filaments may originate at Cape Juby (27°56′N), Cape Boujdor (26°12′N), or in between (Barton et al. 1998). Filaments are linked to upwelling and are therefore more frequent during summer in the north.

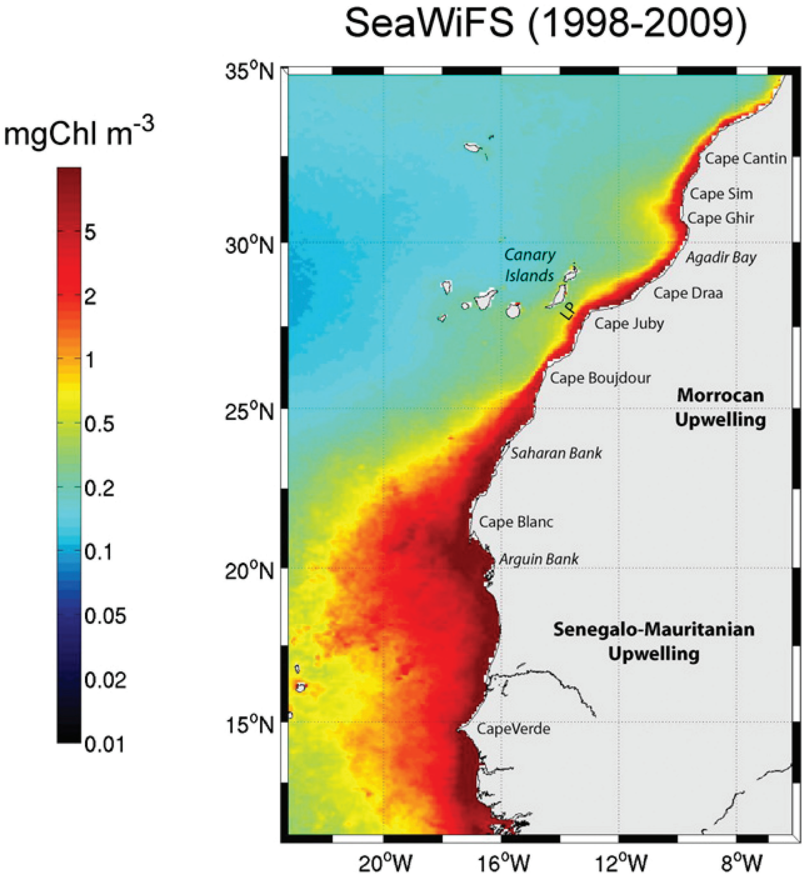

Figure 38 Surface distribution of chlorophyll a obtained from SeaWIFS, averaged over the period 1998–2009 (Auger et al. 2015).

Macromedusae

Species composition

Our knowledge of jellyfish in the Canary Current system is very limited by comparison with that from the other three systems, and mostly of a comparatively qualitative or anecdotal nature. Although jellyfish science in the region is in its infancy, it is already very clear that there are pronounced differences between the fauna of the Canary Current and the balance of the EBC systems.

According to data from the Institut National De Recherche Halieutique (INRH, Morocco) and the Consejo Superior De Investigaciones Científicas (CSIC, Spain) (Prieto & Idrissi 2020), and historic literature from the region, nine species of large jellyfish have been inventoried from the Canary Current system, the most common of which is the cystonect siphonophore *Physalia physalis*. Although this species is recovered throughout, it is more frequently observed in the northern zone, West of Africa. Of the scyphozoans, *Rhizostoma luteum* is now often observed along the Atlantic coast of the Iberian Peninsula (mainly in the Gulf of Cadiz), after having been rediscovered after 60 years without record (Prieto et al. 2013), and its distribution is known to include the Canary Current system (Kienberger & Prieto 2018). *Catostylus tagi*, although typically found further north, is known to occur occasionally in Canary Current system (Jarms & Morandini 2019). *Pelagia noctiluca* and *Chrysaora hysoscella* have both been recorded, with the former being significantly more

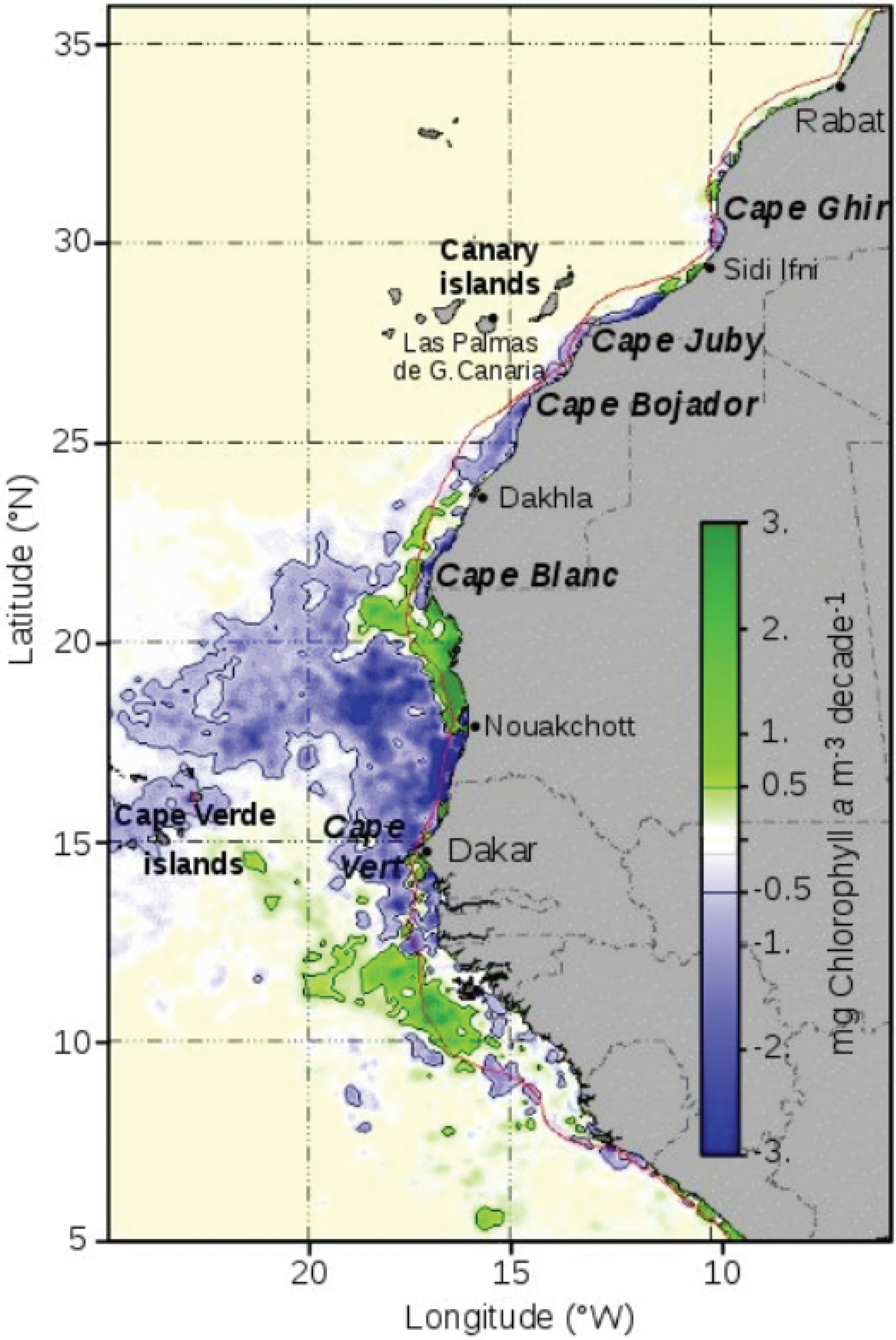

Figure 39 Trends in concentration of chlorophyll (1998–2003) off NW Africa over the period 1998–2003. Data SeaWIFS (Demarcq & Benazzouz 2015).

common than the latter. *Phacellophora camtschatica* is uncommon, as too are a species of *Aurelia* and a species of *Drymonema*. Finally, the cubozoan *Carybdea marsupialis* has a permanent population in the Gulf of Cadiz, and it has been spotted historically in the NW African coast of Morocco (Furnestin 1959). Although species of the hydrozoan *Aequorea* have been noted in the region, they are uncommon. Photographs of the commonly collected species are shown in Supplementary Figure 6.

Distribution

Information on the distribution of macromedusae in space and time is limited, primarily because jellyfish are neither routinely encountered nor measured during regular fishery surveys. Using pooled catch data from a variety of research cruises aboard the Amir Moullay Abdelah, Charif El Idrissi and the RV Dr. Fridtjof Nansen over the period 1998–2017, it would appear that jellyfish are most frequently caught between latitudes 22 and 23°N (Figure 40). Distribution changes seasonally and jellyfish are encountered across the sampling area to 32°N during autumn, but are more restricted (22–26°N) during spring and summer (Figure 40).

The INRH has set up a national programme to monitor gelatinous taxa, through a combination of field surveys and questionnaires. Surveys target commonly frequented beaches and areas most affected by stranding; questionnaires target fishermen, surfers, civil authorities and the local community members. The INRH also has a monitoring network along the Moroccan coastline in order

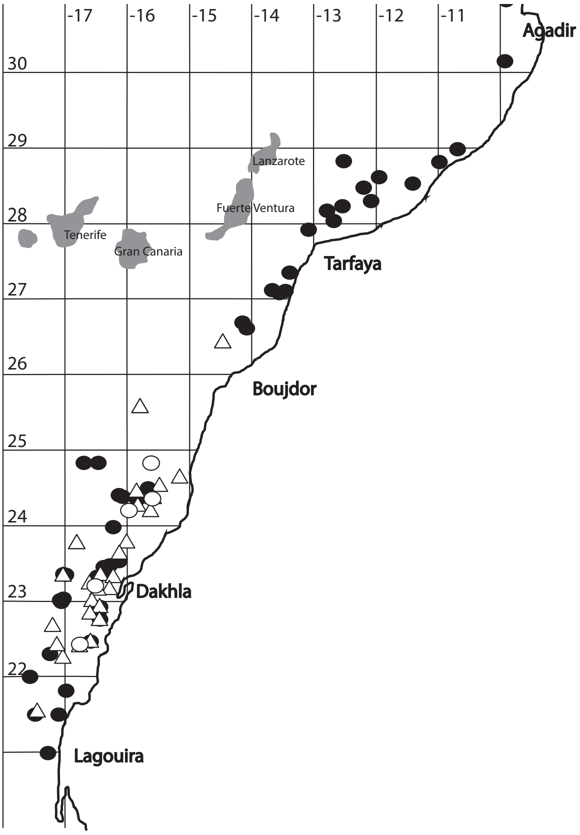

Figure 40 Seasonal distribution of jellyfish catches off the coast of Morocco, 1990–2016: spring (open circles), summer (open triangles), autumn (solid circles) (from Idrissi et al. 2018a).

to follow the development of these species and the evolution of invasions. In addition, land-based observation campaigns have been conducted jointly with the Maritime Fishing Delegations of the districts concerned, local artisanal fishermen's cooperatives and other stakeholders in the marine environment (Mdiq, Casa, El Jadida). The objective of this monitoring programme is to communicate public health alerts and to raise scientific awareness among fishers and other community members, while additionally allowing the collection of baseline biodiversity information.

Stranding data collected along the Atlantic coast of Morocco indicate that the dominant species are *Physalia physalis*, *Pelagia noctiluca* and *Rhizostoma luteum* (Figure 41). *Physalia physalis* appears on shores from February to June, with a maximum in April, while *Pelagia noctiluca* is stranded from June to November, being most frequent during August and September. In the case of *Rhizostoma luteum*, strandings occur in two periods: during March to May and then between September and December. Owing to the tourist value of beaches in the Canary Islands, a network of observers has been established who monitor popular resorts. The extensive data obtained from this monitoring programme confirm that the dominant and recurrent species are *Physalia physalis* and *Pelagia noctiluca* (Prieto & Idrissi 2020). As observed along the coast of Morocco, *Physalia physalis* is present from January to June, with a maximum in March, while *Pelagia noctiluca* is present year-round, with a maximum in November. The numbers of *Physalia physalis* and *Pelagia noctiluca* stranded in the Canary Islands are one and two orders of magnitude larger, respectively, than noted off Morocco (Figure 41).

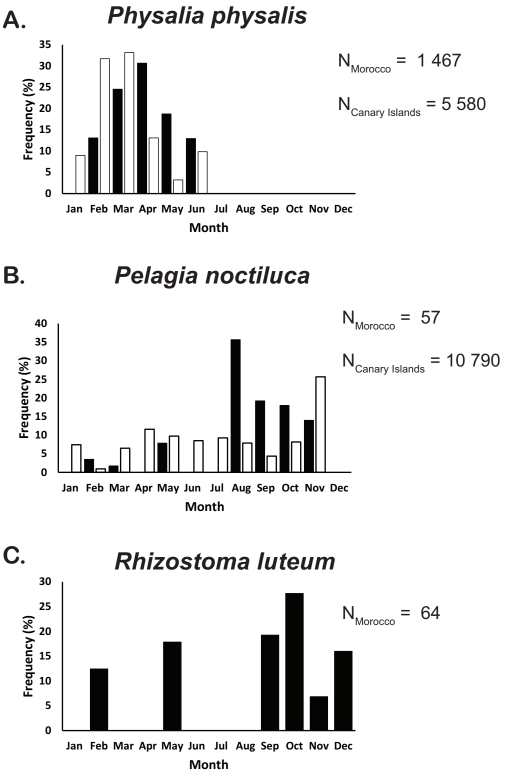

Figure 41 Seasonal changes in the relative abundance (% annual total, *N* shown) of commonly stranded jellyfish observed on the Atlantic coast of Morocco (solid bars) and on targeted beaches in the Canary Islands (open bars): 2009–2019 (Idrissi et al. 2018b, Prieto & Idrissi 2020).

It is very likely, in the case of *Physalia physalis*, that strandings would have followed periods of onshore winds (Shannon & Chapman 1983) and they often occur after strong west or west–north–west winds and very large swells; as has been observed off the Atlantic coast of the Iberian Peninsula (Prieto et al. 2015). Fishers at sea off Oualidia and El Jadida (southern Casablanca) have all confirmed the presence of what they refer to as "Affia" during late winter and spring and indicate that they are most abundant at depths of about 70 m.

Although specimens of medusae are now measured when collected, robust data are missing. Off Ain Diab, El Jadida and Laayoune, it would appear from unpublished data that *Physalia physalis* stranded early in the year have larger floats (mean 14.5 cm) than those stranded in late April and early May (mean 8.8 cm). Furthermore, the majority of individuals collected in winter are mature (70%), whilst only 41% were mature during late spring (INRH unpublished data).

From an analysis of all the data collected along the coastlines of both Morocco and the Canary Islands (Prieto & Idrissi 2020), it would appear that there is a considerable interannual variability in the number of stranded jellyfish (Figure 42), with total numbers reflecting the abundance of *Pelagia noctiluca* rather than *Physalia physalis*. The two dominant species do not appear to fluctuate in tandem, and evidence from further north (the Gulf of Cadiz) indicate that strandings of *Physalia physalis* there are related to very negative values of the North Atlantic Oscillation (NAO) (Prieto et al. 2015). The data are too scarce to demonstrate any clear relationship in the Canary Current system as yet, although the highest numbers of stranded colonies seem to be linked to positive (not negative) NAO indices (Figure 43). *Rhizostoma luteum*, which was absent from stranding records in the Canary Islands, also shows interannual variations in relative abundance but is generally uncommon.

Unfortunately, further information about jellyfish in the Canary Current system, for instance relating to their reproduction or their interactions with humans and fisheries, is entirely lacking, although as in the other EBC systems, jellyfish have been seen to be consumed by benthic scavengers (Supplementary Figure 7). Information on the fatty acid composition of *Rhizostoma luteum* is provided in Supplementary Table 5.

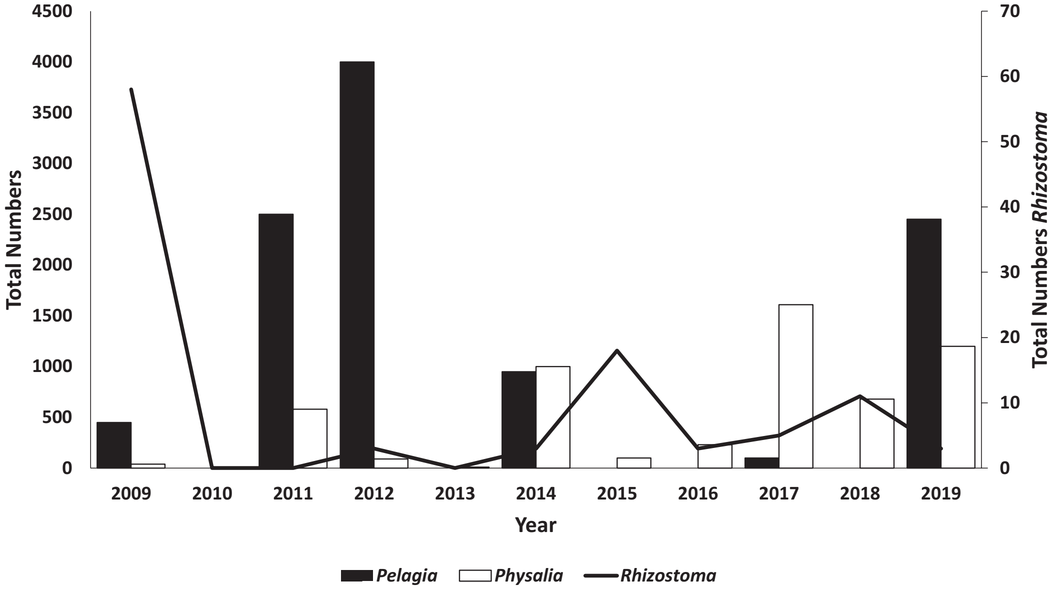

Figure 42 Interannual changes in the numbers of jellyfish stranded in the Canary Current system. Data for *Rhizostoma luteum* recorded only along the coast of Morocco. Data from Idrissi et al. (2018b) and Idrissi (2020).

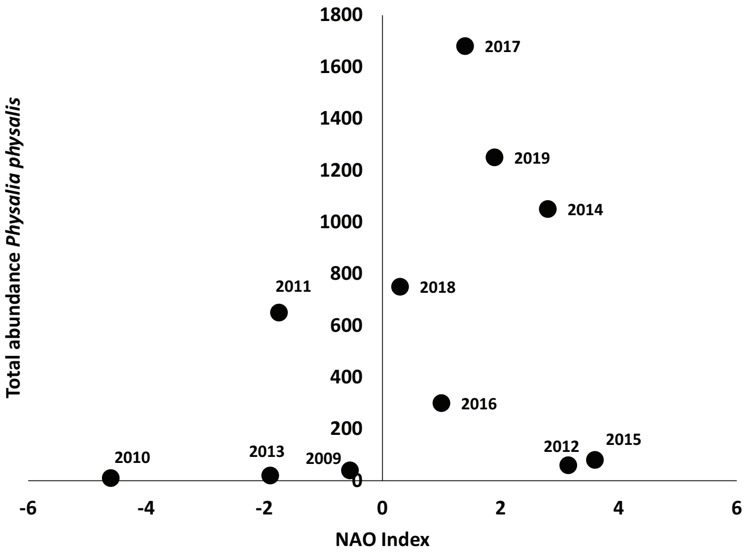

Figure 43 Scatterplot showing the relationship between the total number of stranded *Physalia physalis* recorded in the Canary Current system and the NAO index.

Synthesis

The species

Species of *Chrysaora* and *Aequorea* appear to dominate the macromedusae in three of the four EBC systems, the exception being the Canary Current, where robust data relating to abundance and distribution at the species level are lacking. Whilst our understanding of the phylogenetic relationships among species of *Aequorea* is poor, the same is not true of *Chrysaora* – although the pattern is far from clear. Bayha et al. (2017) have recently indicated that the genus *Chrysaora* is paraphyletic within the family Pelagiidae and argue that if the identity of *Mawia*, *Sanderia* and *Pelagia* is upheld, then it would be necessary to break up what is currently *Chrysaora* and erect an additional three genera to take account of the embedded structure (Bayha et al. 2017). Although these results are in contrast to those by Gershwin & Collins (2002), Morandini & Marques (2010) and Avian et al. (2016), they are based on a comprehensive suite of unambiguous molecular markers (Bayha et al. 2017).

Updated molecular trees are provided here as Figures 44–46, which incorporate the newly recognized *Chrysaora agulhensis* (Ras et al. 2020) and *Chrysaora pseudoocellata* (Mutlu et al. 2020). Sequence data for the COI and 18S gene regions were extracted from GenBank as these were available for the largest number of species. Detailed information around sequences used can be obtained from Supplementary Tables 6 and 7. Gene regions were aligned separately using the Geneious sequence aligner, under default settings, within Geneious v.11.1.4 (https://www.geneious.com). Datasets were then checked using GBLOCKS (Castresana, 2000) and regions with poor alignment were omitted from subsequent analyses. The Akaike and Bayesian information criteria were used in the programme jModeltTest v.2.1.2 (Darriba et al. 2012) to determine the best fit model of substitution for the COI (HKY+I+G), 18S (TrN+G) and a concatenated dataset (GTR+I+G). Datasets were analysed using both Bayesian Inference (BI) and maximum-likelihood (ML) frameworks, separately first and then as a concatenated dataset. Maximum-likelihood analyses were conducted using PhyML v.3.0 (Guindon et al. 2010), and node support was obtained using the substitution models determined previously by performing a 1000 bootstrap replicate analysis. Bayesian analyses were all performed using the BEAST v.2.3.2 software pipeline (Bouckaert et al. 2019), executed on the CIPRES high-performance computing portal v.3.1 (Miller et al. 2010). For the Bayesian analyses, three runs were executed and each run for 100 * 10^6 generations, sampling every 1000th generation. Runs were then checked for adequate chain mixing and convergence using the program Tracer v.1.6 (Rambaut et al. 2018) and 25% of trees discarded as “burnin” using the program LogCombiner v.2.6.3 (Bouckaert et al. 2019). Using TREEANNOTATOR v.2.6.3 (Bouckaert et al. 2019), the 50% maximum clade credibility tree was computed along with the mean branch lengths and posterior probabilities. We then attempted to calibrate a molecular clock onto the COI and concatenated trees using BEAST v.2.6.3 (Bouckaert et al. 2019). For the concatenated dataset, COI and 18S gene regions were analysed under different substitution models as determined earlier but with clock models linked. We also used a birth–death incomplete sampling prior for both datasets and ran the MCMC chain for 200 * 10^6 generations, sampling every 1000th tree. We again followed the steps listed earlier to summarize the trees. All trees were visualized in FIGTREE v.1.4 (Rambaut, 2014). Lastly, mean interclade and intraclade pairwise sequence divergence “P” values were computed using MEGAX v.10.1.8 (Kumar et al. 2018) for the COI gene region and are shown in Supplementary Tables 8 and 9. The above analyses were repeated for available sequences of COI (substitution model: GTR+I+G) for the genus *Rhizostoma (Rhizostoma pulmo*, *Rhizostoma octopus*, *Rhizostoma luteum)* (Supplementary Tables 10 and 11).

Our analyses of *Chrysaora* support previous findings (Gershwin & Collins 2002, Morandini & Marques 2010, Avian et al. 2016, Bayha et al. 2017, Gómez Daglio & Dawson 2017), which define a NE Pacific clade comprising the four species that can be encountered in the California Current as basal. The two most southerly species *Chrysaora achylos* and *Chrysaora colorata* show the lowest levels of pairwise sequence divergence (8.6% ± 1.2, Supplementary Table 8) in this clade, and a potential split between these taxa occurred only ~8.6 million years ago (mya) (Figure 44). The analyses of Bayha et al. (2017) and Gómez Daglio & Dawson (2017) have suggested *Chrysaora melanaster* as the most basal lineage within this NE Pacific clade. Our analyses support this, showing high bootstrap support (100) and posterior probabilities (1) (Figure 45) for the basal placement of *Chrysaora melanaster* in the concatenated analyses. Interpretation of subsequent relationships is clouded by the unresolved position of *Chrysaora chinensis*, an observation in agreement with Bayha et al. (2017). Within the COI tree (Figure 44), *Chrysaora chinensis* is basal to all remaining taxa (low bootstrap support (51%) and posterior probability (0.35)), which is in agreement with the analyses of Gómez Daglio & Dawson (2017). However, the high bootstrap support (100%) and posterior probabilities (1) within the concatenated analyses (Figure 45) suggest *Chrysaora chinensis* is more likely to be basal to the clade comprising *Chrysaora pacifica*, *Chrysaora africana* and *Chrysaora pseudoocellata*. Regardless, the existence of a pan-Pacific ancestor enjoying a distribution in warm waters is not unlikely.

Our analyses consistently place *Chrysaora pacifica* basally in the East Atlantic clade with *Chrysaora africana* and *Chrysaora pseudoocellata*, and a split between these lineages took place ~32–67 mya (Figures 43 and 44). The palaeoceanographic processes that might have accompanied divergence are unknown, but could reflect the formation of the Bay of Bengal (Hu et al. 2017) and subsequent eastward movement along the East African coast to the South-East Atlantic. The pattern observed is not unlike that noted for *Pelagia noctiluca* by Ale et al. (2019), who showed populations from the Indian Ocean to be basal to those collected off southern Africa which in turn were basal to those of the North Atlantic.

Chrysaora quinquecirrha and *Chrysaora lactea* appear to be ancestral to the remaining clade, splitting from populations in the (likely) equatorial Pacific some ~64 mya (Figures 43 and 44). Speculating, this loosely coincides with timing of an asteroid impact in Mexico, which created very different environments on either side of the impact site (Smit & Hertogen 1980). This in turn could have led to the further separation of populations now invading the North-East Atlantic: some spreading northward and diverging into *Chrysaora quinquecirrha*, others moving southwards to

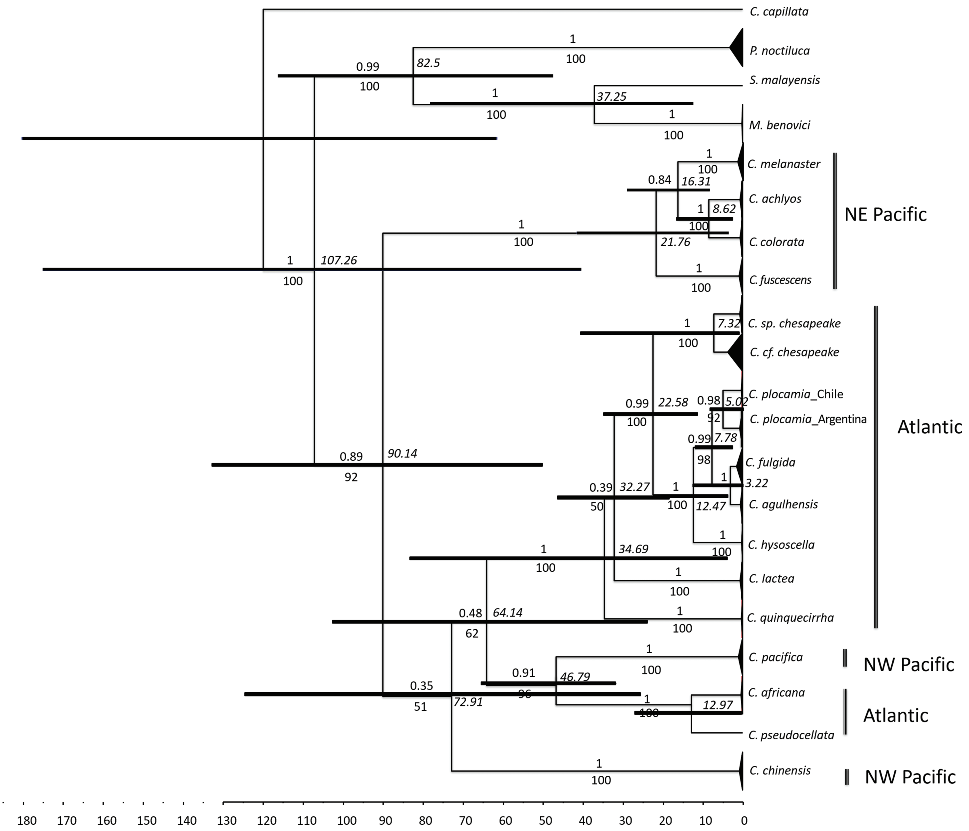

Figure 44 Rooted time calibrated phylogeny for all putative taxa within the genus *Chrysaora*, based on the COI gene region, extracted from GenBank. Sequences for *Mawia* and *Pelagia* have been included here as well for a total of 132 sequences. All analyses performed using BEAST v.2.3.2 (Bouckaert et al., 2019). Posterior probabilities are shown above branches while bootstrap support values are given below branches. Estimated divergence times are represented adjacent to nodes and node_height_95%HD applied to all internal nodes to display error rates. Scale is represented in mya. The tree has been shaded in order to illustrate well-supported lineages. Detailed information around the sequence data can be obtained from Supplementary Table 6.

eventually form *Chrysaora lactea*. Whilst the latter species does not appear at this stage to have undergone any further diversification, the taxa occurring within the North-West Atlantic appear to have been a source for those in the North-East (*Chrysaora hysoscella*) and then South Atlantic (*Chrysaora fulgida*, *Chrysaora agulhensis* and *Chrysaora plocamia*).

Our analyses consistently place *Chrysaora plocamia* from the South-West Atlantic and South-East Pacific in a close relationship with, but basal to, taxa from the South-East Atlantic (*Chrysaora fulgida* and *Chrysaora agulhensis*). Bayha et al. (2017) made similar observations, and our data indicate a potential divergence of *Chrysaora plocamia* around ~8 mya within the COI tree and an earlier split of ~16 mya within the concatenated tree. There are relatively low mean pairwise sequence divergences between *Chrysaora plocamia* and the South-East Atlantic species (~7%, Supplementary Table 8), and only slightly higher values (~9%, S3) are noted with *Chrysaora hysoscella* in the North-East Atlantic. Pairwise sequence divergences also revealed pairwise differences of 3.7%±0.6% between *Chrysaora plocamia* collected off the coast of Chile and those from Argentina. Dispersal is clearly a driver of diversification.

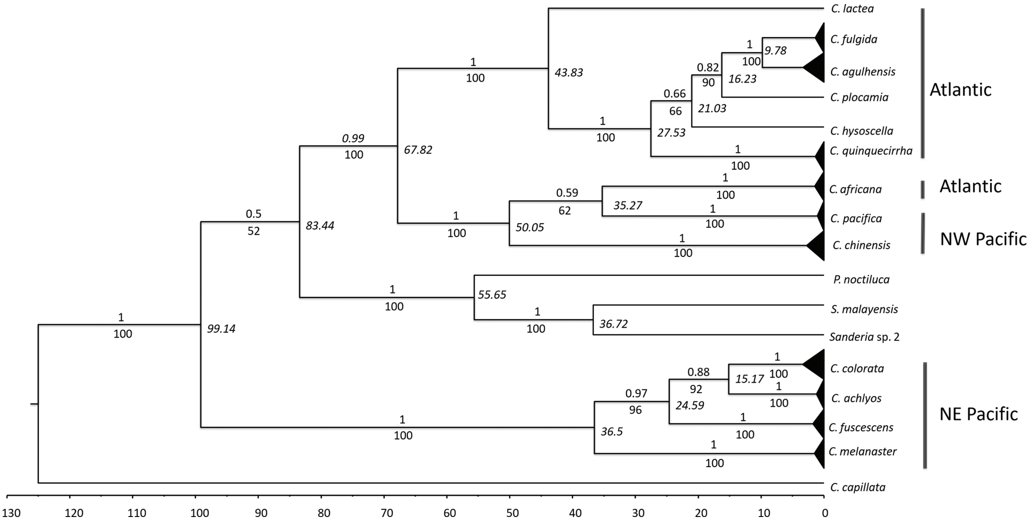

Figure 45 Rooted time calibrated phylogeny for all putative taxa within the genus *Chrysaora*, based on a concatenated dataset of COI and 18S gene regions, for a total of 50 individuals across various taxa within the *Chrysaora, Mawia* and *Pelagia*. Detailed information around the sequence data can be obtained from Supplementary Table 6. All analyses performed using BEAST v.2.3.2 (Bouckaert et al., 2019). Posterior probabilities are shown above branches, while bootstrap support values are given below branches. Estimated divergence times are represented adjacent to nodes. The tree has been shaded in order to illustrate well-supported lineages. Scale is represented in mya.

As previously noted, although species of *Chrysaora* dominate most EBC systems, this is not the case within the Canary Current system. Based on the close relationship between population in the South Atlantic, it is possible this system presents a recent break in gene flow between the northern and southern taxa. That does not mean to say that *Chrysaora* are not present in this system, because "during research vessel survey El Awam-IMROP, carried [out] in May 2014, a bloom of jellyfish, probably *Chrysaora fulgida*, which is probably a new species for the area, was observed in southern Mauritania's EEZ" (Inejih et al. 2014). Whilst we doubt that the named species was in fact *Chrysaora fulgida* (it was probably *Chrysaora hysoscella*, Supplementary Figure 6), the observation suggests that this species' rarity may be controlled by unknown environmental factors.

The genus *Rhizostoma*, which is widespread within the Mediterranean and North-East Atlantic, encompasses only three formally accepted taxa: *Rhizostoma pulmo*, *Rhizostoma octopus* and *Rhizostoma luteum* (Jarms & Morandini 2019). In both the Bayesian inference and maximum-likelihood analyses, *Rhizostoma luteum* is basal to the other two species, with the latter two showing a low mean pairwise divergence of only 5.4%±0.01 (Figure 46, Supplementary Tables 10 and 11). *Rhizostoma pulmo* and *Rhizostoma octopus* have been shown to have overlapping distributions, and the low pairwise divergence between the species suggests they may have diverged more recently. Within *Rhizostoma luteum*, our analyses revealed specimens from the South-East Atlantic have fewer nucleotide substitutions per site than those off North Africa and the western Mediterranean. As this species has also been recorded in the South-West Indian Ocean, it is not unlikely, given parallel patterns observed in *Pelagia* and *Chrysaora* (*pacifica, africana, pseudoocellata*) that colonization of the North-East Atlantic followed similar dispersal routes resulting in the patterns observed within their DNA.

As noted previously, the sardine *Sardinops sagax* (Bowen and Grant 1997) and species of the anchovy *Engraulis* (Grant et al. 2005, Silva et al. 2014) often dominate the biomass of small pelagic fishes in EBC systems, although they are not exclusively associated with them. Recent dispersal

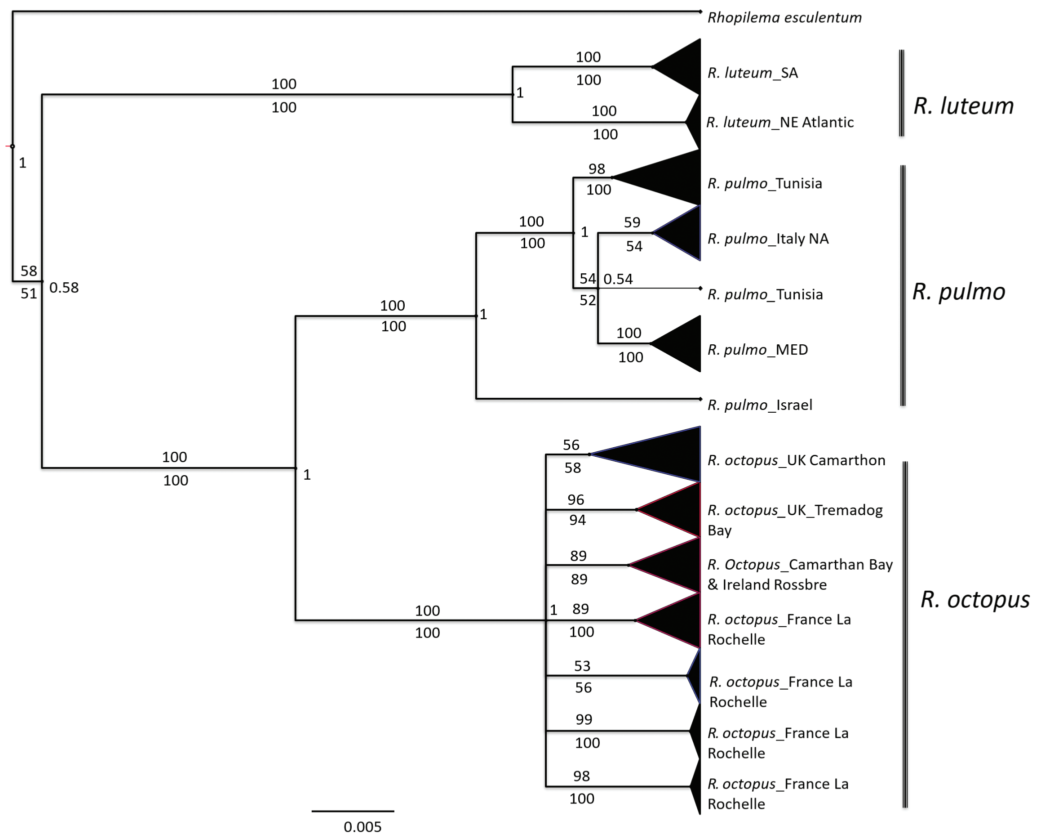

Figure 46 Maximum clade credibility BI tree, inferred using a dataset of 136 COI sequences for all putative taxa within the genus *Rhizostoma*, obtained from GenBank for various localities. Bayesian (BI) analyses performed using BEAST v.2.3.2 (Bouckaert et al., 2019); maximum-likelihood (ML) analyses performed in PhyML v.3.0 (Guindon et al., 2010). Bootstrap support values (BI) are shown above branches, while bootstrap support from the ML analysis are shown below branches. Posterior probabilities are displayed next to nodes. The tree has been shaded in order to illustrate well-supported lineages. Subtrees have been collapsed to improve readability, but detailed information around included sequence data can be obtained from Supplementary Table 7.

along the narrow, western margins of continental land masses, rather than vicariance, has been proposed to explain these distribution patterns (Bowen et al. 2016): the equator clearly having been a leaky barrier to antitopicality. The copepod *Calanoides nasutus* occurs in both the Canary and Benguela EBC systems (Viñas et al. 2015), where it may dominate mesozooplankton biomass (Peterson 1998). Although there are some differences in the genetic structure of populations of *Calanus nasutus* in the two Hemispheres, trans-equatorial dispersal is believed to maintain species integrity in the present (Höring et al. 2017). It has also been suggested that “founder dispersal may have played a major role in the generation of the current disjunct geographical distribution” among the four species of *Nyctiphanes*: three of which are also associated with EBC systems (D’Amato et al. 2008). Similar patterns have been described here for the *Chrysaora*.

The point of this wander off the beaten track is that some of the ecological characteristics of the different key species in the three EBCs that support populations of *Chrysaora* may have their roots in the different ancestries of the taxa involved. *Chrysaora fuscescens* in the California Current lacks richly folded oral arms and reaches a maximum size of only about 60 cm. By contrast, both *Chrysaora fulgida* and *Chrysaora plocamia* possess lush oral arms and may approach 1 m in diameter.

We should be careful not to over-generalize, as Abboud et al. (2018) have shown there can be significant genetic structuring within jellyfish populations of LMEs. These authors noted that this was especially pronounced within the California Current system[6] and in the genera *Aequorea* and *Chrysaora*: with some populations less than 1000 km distant from each other being quite distinct (Abboud et al. 2018).

Although the important marine resources within EBC systems may fail to display genetic substructure (e.g. Healey et al. 2020), it should be remembered that they are motile with different age groups using different parts of the wider system (e.g. Strømme et al. 2016). Fréon et al. (2009) implied that the major EBCs are neither latitudinally nor longitudinally homogeneous and as we have summarized above, different areas of each system have distinctly different environments, especially for organisms that are meroplanktonic, and whose benthic life-history stage is so closely tied to the benthos in shallow water. The data reviewed above suggest, perhaps not surprisingly, that there are regional differences in the ecology of populations within each system. In the Benguela Current system, for example, there is evidence of seasonality in the timing of reproduction by adult *Chrysaora fulgida* off Lüderitz, but not at Walvis Bay; there are differences too in the timing of strobilation (as evidenced by the presence of ephyrae in the water column) between Lüderitz and Walvis Bay. In the Humboldt system, *Chrysaora plocamia* shows a pronounced seasonality in appearance off Peru, which is at odds with that argued to be shown by populations off Chile. These differences may reflect localized adaptations to the local environment, but if there are barriers to mixing, then there is no reason to suppose that these differences may not become genetically fixed.

Following the methods employed by Abboud et al. (2018), our data for the Benguela Current ecosystem indicate significant geographic structure within populations of *Chrysaora fulgida*. This is most obvious at the southern boundary to the system, where *Chrysaora agulhensis* has recently been shown to have evolved from a common ancestor with *Chrysaora fulgida* only ~3 mya. The Agulhas Bank along the south coast of South Africa is environmentally distinct from that along the west coast, being influenced by the subtropical Agulhas Current, and local adaptations to the environment there have led to fixed genetic differences with respect to populations of *Chrysaora fulgida* in the Benguela *sensu stricto*. Interestingly, similarly large genetic differences appear to exist at the northern border of the Benguela, which influenced the subtropical Angola Current, with populations of *Chrysaora fulgida* north of Walvis Bay being ~1.2% ± 0.3% different (pairwise sequence divergence) from those to the south (Ras et al. unpublished data). Unsurprisingly too is the fact that populations of *Chrysaora plocamia* off the coast of Argentina are 3.7% different from those off Chile. As Abboud et al. (2018) note "analyses relying on fixed areas, such as LMEs, or a fixed geographic scale … are pragmatic but will often be mismatched to the actual scales and natural boundaries of jellyfish population structure. As a result, such analyses will often be mismatched to the actual scales, drivers, and consequences of jellyfish blooms" (Abboud et al. 2018, pp. 212).

The ecological role that jellyfish play in EBC systems: a synthesis

Large medusae are likely to play a critical, although poorly understood role in upwelling systems around the world. During bloom conditions, they are known to consume prodigious quantities of zooplankton that would otherwise be available for mid-trophic-level consumers that are utilized by larger fishes, seabirds and marine mammals and in some cases directly by humans (Robinson et al. 2014), thus indirectly affecting foodweb structure and fisheries production. A more direct negative effect on fish results from predation of medusae on early life stages of fish species (Purcell & Arai 2001), although assessing the impacts on fish populations has generally been attempted on a local scale (Möller 1984, Fancett & Jenkins 1988, Purcell 1989, Purcell & Grover 1990). Estimates of total numbers of a given larvae consumed in an ecosystem expressed as a percentage of total have been made in some larger shelf ecosystems (e.g. Brodeur et al. 2002, Tilves et al. 2016), but similar direct estimates have not been attempted in upwelling ecosystems. Fortunately, many larger medusae attain their peak biomass and likely consumption rates relatively late in the summer; hence, they are unlikely to overlap with the egg and larval stages of most fish species which spawn more often in non-upwelling seasons (see Suchman et al. 2008, Zeman et al. 2016). This may not be the case however in the Benguela system when peak biomass occurs when some fish species are known to spawn (Flynn et al. 2012). Therefore, predation impact on early life stages of fish by immature stages of medusae may be a significant source of mortality, but this interaction has not been examined in detail for any of the systems examined here.

Competition for limited prey resources is likely to have a more pronounced effect on many fish species, but it also much more difficult to quantify. Opdal et al. (2019) used time series data and energy consumption relationships to examine the relationship between jellyfish, forage fishes and available zooplankton in several ecosystems including the California Current and Benguela Current, and found little support for the hypothesis that jellyfish were trophically replacing forage fishes. In a more direct approach, several attempts have been made to examine the diet overlap and potential competition between large medusae and pelagic fishes (Purcell & Sturdevant 2001, Brodeur et al. 2008b). This has been stimulated by the observation of an inverse relationship between time series of abundances of macromedusae and small pelagic fishes (Brodeur et al. 2002, 2008b, 2014, Robinson et al. 2014). The spatial and trophic overlap of two large medusae, *Chrysaora fuscescens* and *Aurelia labiata*, and several pelagic fishes in the upwelling region of the Northern California Current was examined during late summer by Brodeur et al. (2008b). Diet overlap (based on stomach analyses and stable isotope ratios) was substantial for several key forage species, including Pacific sardine, Pacific herring, Pacific saury and northern anchovy due to a similar utilization of small copepods and euphausiid larvae. Combined with a measure of geospatial overlap, these species were considered by Brodeur et al. (2008b) to have the greatest potential to compete with both jellyfish species.

Although the interactions between jellyfish and other predators often appear to be negative, there are some benefits to fish from having large numbers of gelatinous zooplankton present. One is the notable importance of jellyfish as a food source for many upper trophic-level organisms, which is receiving new scrutiny with the use of alternative biochemical and genetic methods of examining predator–prey interactions (van der Bank et al. 2011, Cardona et al. 2012, Lamb et al. 2017, Hays et al. 2018, Marques et al. 2019). Anomalous increases in gelatinous zooplankton in upwelling systems could enhance production of species adapted to feeding on them (Utne-Palm et al. 2010) or lead to trophic shifts to gelatinous prey in normally crustacean feeding fishes (Brodeur et al. 2019). Another well-documented interaction between jellyfish and some fish species is the association of early life stages of fish with cnidarians (Purcell & Arai 2001). Griffin et al. (2019) reviewed the literature on this and found that jellyfish provide habitat for larval and juvenile fishes, many of which are commercially important, using their hosts for protection from predators as well as opportunistically feeding upon their hosts captured prey, which may lead to reduced fish mortality and increased recruitment. Although it is likely that a number of fish may be commensal with macromedusae in the systems examined here, this has not been the subject of extensive study up to this point.

Jellyfish, fisheries and climate: a synthesis

Using data available at the time, Bakun (1990) first highlighted the idea that an increase in global temperature would result in intensified upwelling, effectively as a result of the stronger atmospheric pressure gradients that are anticipated to develop between land and sea. While he suggested this would be accompanied by increased phytoplankton production, he emphasized the lack of certainty about the fate of this production, indicating it could be diverted to mesopelagic rather than epipelagic species and that it could result in increased organic sedimentation and an elevated chance of hypoxia (Bakun 1990). The Bakun Hypothesis, as it subsequently became known, has been elaborated upon by a number of authors in the intervening years (e.g. Snyder et al. 2003, García-Reyes et al. 2015, Sydeman et al. 2014, Wang et al. 2015), and although there have been some modifications to the detail, it has been widely accepted.

In their most recent contribution to the subject, Bakun et al. (2015) summarized the scenario thus: "anticipated changes include the poleward migration of the Oceanic High and source waters. Continental thermal lows are anticipated to deepen, which will intensify upwelling-favo[u]rable (equatorward) winds. Changes in the water column include greater stratification, greater rates of upwelling, and greater offshore transport as well as the offshore migration of the upwelling front" (Bakun et al. 2015; pp. 88). Although the exact implications of these anticipated changes are still unclear, Bakun et al. (2015) suggested they could include changes in the composition and production of autotrophs (hence too, heterotrophs), spatial and temporal mismatches between production and consumption, and changes in species distributions; the latter in part reflecting elevated anoxia and acidification, as well as changes in the distribution of prey. These, and other authors, have stressed that EBC systems are naturally variable, and as such may be resilient to some of these changes (Bakun et al. 2015, García-Reyes et al. 2015) in the absence of over-exploitation or additional major anthropogenic impacts (Bakun et al. 2015; our emphasis). Bakun et al. (2015) also noted that "shifts toward an increasing dominance by zooplanktivores", such as jellyfish, could lead to unpredictable and/or undesirable (from a human perspective) ecosystem states as "more versatile components … might successfully exploit opportune ecological loopholes that develop" (Bakun et al. 2015; pp. 91). The latter statement could be interpreted in the context of predator-free space, and in the case of jellyfish, it could effectively lead to the former: jellyfish enjoying such space in the absence of pelagic fishes that could then lead them to become dominant zooplanktivores (see e.g. Bakun 2006, Richardson et al. 2009).

Following Mills (2001), a number of (perhaps now dated) papers were published in the first decade of the twenty-first century that attempted to synthesize what we knew about jellyfish populations globally at the time (e.g. Purcell et al. 2007, Richardson et al. 2009). One of the key take-home messages from these two papers, in particular, was that jellyfish have a suite of adaptations that could enable them to take advantage of marine environments that have been modified in the Anthropocene: (some species have) a remarkable tolerance to low concentrations of dissolved oxygen as medusae and polyps; many species can feed across a very wide range of prey, including protistans, efficiently (Acuña et al. 2011); warming seas can promote individual and population growth (of some, but not all, species) (Boero et al. 2016), and the proliferation of hard substrata associated with coastal development, energy and aquaculture increases the opportunities for the settlement of polyps (Duarte et al. 2012).

With the exception of the latter, which is generic across all coastal systems, Bakun et al.'s (2015) scenarios talk directly to some of the adaptations of (some) jellyfish. Increased levels of hypoxia may benefit some jellyfish as they do not appear to be affected by low oxygen conditions as fishes are, with notable exceptions (Salvanes et al. 2015). Indeed, low oxygen has been shown to enhance jellyfish predation on fish larvae compared to fish predation on the same larvae (Shoji et al. 2005). An increase in temperature will place stress on both predation and competition between forage fishes and jellyfish in EBC systems by increasing the feeding and growth rates of some medusae and changing the structure of the plankton assemblages. A change in the characteristics (temperature, salinity, oxygen) of nearshore bottom water may stimulate/inhibit ephyra production, although subsequent offshore losses may weaken coastal populations. However, much of this is speculation and we must be cautious about making generalizations (Pitt et al. 2018). After all, while a warming sea may favour budding by scyphopolyps, it may decrease opportunities for strobilation and the actual recruitment of jellyfish (Lynam et al. 2004).

Although changes in global temperature will have an impact on climate-scale systems such as El Niño Southern Oscillation (ENSO), exactly how they will be affected is unclear (Bakun et al.

2015). In the Humboldt Current system, the spatial distribution and abundance of *Chrysaora plocamia* are both expected to increase during El Niño years and decrease during La Niña years (Quiñones et al. 2015). By contrast, populations of most cold-water species are expected to decrease in the California Current system during warming periods, but increase during cooler ones (Pearcy et al. 1985, Heitstuman 1994). Although comparable information for the Atlantic EBC systems is missing, it is clear that there is no "one-size-fits-all" explanation. Again, we need to be cautious.

In attempting to understand the likely effects of climate change on EBC systems, we cannot realistically ignore the simultaneous impacts of fisheries, especially for small pelagic fishes. And the text highlighted above, in reference to the conclusions of Bakun et al. (2015), is a reference to the situation off Namibia in the northern Benguela Current system (Roux et al. 2013). However, it is by no means clear that all EBC systems would behave similarly. Using a 40-year time series (1972–2014), Quiñones et al. (2015) examined the response of *Chrysaora plocamia* to both environmental variability and fishing pressure in the northern Humboldt Current system at a number of different timescales. Their results show that fluctuations in the biomass of *Chrysaora plocamia* were related to the environment, but not with the landings of anchoveta. Jellyfish biomasses were high and variable during the El Viejo warm regime in the 1970s and 1980s but low during the La Vieja cold regime known during the 1990s and 2000s (Quiñones et al. 2015). At shorter timescales and within the El Viejo regime, the peaks of jellyfish abundance coincided with events related to El Niño Southern Oscillation (ENSO). Anchoveta landings and the number of annual trips in the industrial fishery increased by a factor of three in the 1990s and 2000s, when jellyfish were scarce, but during the period of the greatest jellyfish abundance (1970s and 1980s), fishing pressure was low (Quiñones et al. 2015).

The northern Humboldt Current system is unique in its susceptibility to extreme interannual disturbances associated with the ENSO phenomenon, yet re-accommodates and recovers quickly without any apparent lasting impact (Bakun & Weeks 2008). Part of the reason for this may lie not so much with jellyfish but with the balance of key pelagic components. In the northern Humboldt Current system, the main pelagic resource is the anchoveta, which reaches age of first sexual maturity at one year in Peru (Perea & Roque 2005). Their short life provides anchoveta populations with an in-built resilience in the face of significant exploitation. By contrast in the northern Benguela Current system, sardine become sexually mature at two years of age (van der Lingen et al. 2006). Jellyfish are not common in the southern Benguela Current system off South Africa, perhaps because there are several species of small pelagic fish (anchovy and sardine) that occupy a similar niche, whilst off Namibia there has characteristically been just one: sardine (Boyer et al. 2001). The southern Benguela Current system is characterized by a narrow shelf and already pronounced offshore advection, whilst the broader shelf off central Namibia is remarkable for its retention mechanisms: the latter contributing to the build-up of coastal jellyfish populations.

Gaps in knowledge and constraints

Attempts to understand any species in any system require a sound knowledge of population dynamics. Sadly, the lack of targeted support for research into jellyfish means that the data on which our understanding is based are primarily derived from the by-catch of targeted fisheries surveys (Flynn et al. 2012, Brodeur et al. 2016). While "beggars can't be choosers", using fisheries surveys that are not specifically designed to quantify the structure of jellyfish populations has its limitations. When and where fisheries surveys are undertaken, what depths are sampled, and which gears are used are all dependant on the fish population of interest – not on the by-catch of jellyfish! While the ecosystem approach to fisheries management requires that we change our perception of jellyfish, and indeed much of the information showcased here illustrates that attention, more can and should be done.

Condon et al. (2013) have emphasized the value of collecting data that can contribute towards time series, because it is only with time series that we can measure change. Of course, it would be ideal to have a common set of standards, but the reality is that we are collecting by-catch data from different fisheries using different methods at different times of the year. Attempts to reduce the resulting data to a common standard will be no less fraught than using relative data, which, given the size of the commercial fleets operating in EBC systems, can be easily collected (see e.g. Flynn et al. 2012). Such data would, through time, allow us to explore regional links between population dynamics and both oceanographic/atmospheric conditions and other resources, and would also allow us to track what is happening outside of the time of year when fisheries-independent surveys are conducted. Relative data can also be collected using various community science programmes, as has been quite successfully deployed both more widely (Canepa et al. 2016) and more specifically (Benedetti-Cecchi et al. 2015) in the Mediterranean Sea. However, for such programmes to be useful, it is vital that they be maintained for the long term (Tredick et al. 2017).

The role of jellyfish in an ecosystem may be examined using dynamic simulations incorporated into dynamic mass balance or end-to-end models of whole systems. Although jellyfish were often omitted or underrepresented in early holistic ecosystem models (Pauly et al. 2009), recent iterations have included more robust estimates of abundance and trophic impacts and have shown the importance of this group to many systems globally (Lamb et al. 2019). Such models have been developed for the some of the systems examined here (e.g. Ruzicka et al. 2007, 2012, Brodeur et al. 2011, Robinson et al. 2014, Chiaverano et al. 2018) and have been used to examine different scenarios of increasing or decreasing jellyfish biomass on system functioning. While dynamic ecosystem models are in their infancy and subject to valid criticism (e.g. Boero 2013), our understanding of jellyfish roles in upwelling ecosystems can only benefit from a more complete incorporation of realistic jellyfish biomass and physiology.

Similarly, the role of jellyfish (and other gelatinous zooplankton) in carbon flux throughout the global ocean also requires more robust estimates of jellyfish abundance, physiology and trophic ecology. Recent evaluations indicate that the role of cnidarians, ctenophores and pelagic tunicates in marine carbon export to the benthos (through both carcass depositions and faecal flux) is likely to have been substantially underestimated (Wright et al. 2020), particularly for larger organisms not included in sediment trap estimates of carbon flux (Luo et al. 2020). Thus, a more accurate assessment of the role of jellyfish and other gelatinous zooplankton in EBC foodwebs is important to improving climate models and evaluating the role of carbon cycles in marine systems processes for climate change evaluation (e.g. Pauly et al. 2009).

As Gibbons & Richardson (2013) point out, studies of macromedusae are fraught because of their often-large size. This means that estimates of physiological parameters, especially those associated with feeding, are either based on more tractable, small individuals (e.g. Hansson et al. 2005) or on indirect measures (e.g. Purcell 2009, 2010). Efforts to address this shortcoming are desperately needed, as they would not only provide empirical validation of model outputs but also generate more explicit information about the interactions between species. Although stable isotopes ($\delta^{15}N$, $\delta^{13}C$) are potentially useful tools that can be used to place jellyfish in the context of their trophic environment, there are controversies over fractionation (Post 2002 *cf* D'Ambra et al. 2014), which serve to question their value (e.g. Wang et al. 2020).

We also know little about the interaction between life-history traits and population dynamics over different spatial and temporal scales. In fact, we tend to ignore the life cycle of jellyfish altogether (e.g. Wright et al. 2020), primarily because we know almost nothing about polyps. Indeed, polyps can be regarded as the "elephants in the room", which make jellyfish so different from other members of the plankton (Boero et al. 2008). While they are relatively easy to obtain by artificial means (e.g. Widmer 2008a) and are amenable to laboratory experimentation (e.g. Lucas et al. 2012), they have never been found *in situ* in any EBC system. Experiments on planula settlement have been widely conducted (Lucas et al. 2012), and there is an intuitive understanding of where polyps should be located, but as yet no serious searches have been conducted. However, we should be emboldened by Serrano's (2016) success in using settling plates to study *Chrysaora quinquecirrha* in Barnegat Bay, New Jersey, and renew our efforts. But if studies on polyps *in situ* cannot be conducted (Di Camillo et al. 2010), we could (at least) work on ephyrae as proxies for polyps, since they are identifiable in some of the EBC systems considered here (Widmer 2008b, Skrypzeck 2019). That said, with the exception of the very localized studies conducted off Namibia, routine and regular plankton collections are not being made. We do not deny the great advances in plankton ecology that have been made using the data collected by e.g. the California Cooperative Oceanic Fisheries Investigations (CALCOFI) (Gallo et al. 2019), but in truth, these samples are not collected close enough to the shore to yield useful information on ephyrae. While we remember that the CALCOFI programme was designed to answer questions relating to the interactions between the environment and economically valuable fish resources, the mismatch between fish needs and jellyfish needs is nevertheless frustrating. At the end of the day, however, without a knowledge of polyps *in situ*, we are denied an opportunity to fully understand wild populations (Gibbons et al. 2015). And this is a problem because, as the management of marine systems moves towards Ecosystem-Based Management, jellyfish may serve as an important indicator species for changing ecosystems worldwide (e.g. Samhouri et al. 2010).

But perhaps one of the biggest challenges facing jellyfish science in EBC systems relates to a lack of human capacity. The current number of specialists is too low to cover such a vast region, and the number of specialists on particular taxa is even lower. We believe that training in the taxonomy and ecology of gelatinous zooplankton, and stretching the gap between researchers from different fields (jellyfish researchers, physical oceanographers and fishery biologists), fishers, journalists and policymakers are essential to develop a better understanding of the ecological roles of jellyfish in the marine ecosystems. Such integration will be a critical element in the development of an ecosystem-based approach to fisheries management and to understand the importance of jellyfish in ecosystem functioning.

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Notes

1. Thirty-four specimens of Aequorea forskalea were, however, washed up stranded in the lagoon during January 2014: they ranged in sizes of 8–22 cm, with one specimen being 3 cm.
2. But see also Mohamed et al. (2019) for information on early gametogenesis in *Carybdea murrayana*
3. Podocysts are cysts that form at the base of the polyp that can then remain dormant when environmental conditions are inhospitable and that will form polyps when conditions are favourable.
4. Detailed information on the morphology and development of ephyrae of *Chrysaora fulgida* and *Chrysaora africana* can be found in Skrypzeck (2019), who noted six distinguishable ephyral stages. Stage 0 are newly released and least developed, while Stage 5 are most developed. As an individual grows and increases in size, so it develops increasingly more complex and medusa-like. A meta-ephyra stage is observed immediately before the individual becomes a medusa.
5. https://www.nwfsc.noaa.gov/research/divisions/fe/estuarine/oeip/g-forecast.cfm#TableSF-02.
6. Neither the Humboldt nor the Benguela LMEs were included in the analysis of Abboud et al. (2018).

References

Abboud, S.S., Gómez Daglio, L. & Dawson, M.N. 2018. A global estimate of genetic and geographic differentiation in macromedusae— implications for identifying the causes of jellyfish blooms. *Marine Ecology Progress Series* **591**, 199–216.

Acuña, J.L., Lopez-Urrutia, A. & Colin, S. 2011. Faking giants: The evolution of high prey clearance rates in jellyfishes. *Science* **333**, 1627–1629.

Adams, P.B. 1987. Diet of widow rockfish (*Sebastes entomelas*) in northern California. In *Widow Rockfish: Proceedings of a Workshop*, Tiburon, California, W.H. Lenarz &and D.R. Gunderson (eds). *NOAA Technical Report NMFS* **48**.

Adler, A. & Jarms, G. 2009. New insights into reproductive traits of scyphozoans: Special methods of propagation in *Sanderia malayensis* GOETTE, 1886 (Pelagiidae, Semaeostomeae) enable establishing a new classification of asexual reproduction in the class Scyphozoa. *Marine Biology* **156**, 1411–1420.

Aguilera, M.A., Aburto J.A., Bravo L., Broitman, B.R., García, R.A., Gaymer, C.F., Gelcich, S., López, B.A., Montecino, V., Pauchard, A., Ramos, M., Rutllant, J.A., Sáez, C.A., Valdivia, N. & Thiel, M. 2019. Chile: Environmental status and future perspectives. In *World Seas: An Environmental Evaluation*, C. Sheppard (ed.). United Kingdom: Academic Press, Seco2nd Eedition, pp. 673–702.

Albert, D.J. 2005. Reproduction and longevity of *Aurelia labiata* in Roscoe Bay, a small bay on the Pacific coast of Canada. *Journal of the Marine Biological Association of the United Kingdom* **85**, 575–581.

Ale, E., Ramšak, A., Stanković, D., Morandini, A.C., Meyer, D. & Marques, A.C. 2019. Early Pleistocene divergence of *Pelagia noctiluca* populations (Cnidaria, Medusozoa) between the Atlantic Ocean and the Mediterranean Sea. *Journal of Marine Biology Association UK* **99**, 1753–1764.

Alfaro-Shigueto, J., Mangel, J.C., Pajuelo, M., Dutton, P.H., Seminoff, J.A. & Godley, B.J. 2010. Where small can have a large impact: Structure and characterization of small-scale fisheries in Peru. *Fisheries Research* **106**, 8–17.

Alfaro-Shigueto, J., Mangel, J.C., Bernedo, F., Dutton, P.H., Seminoff, J.A. & Godley, B.J. 2011. Small-scale fisheries of Peru: A major sink for marine turtles in the Pacific. *Journal* of *Applied Ecology* **48**, 1432–1440.

Alheit, J. & Niquen, M. 2004. Regime shifts in the Humboldt Current ecosystem. *Progress in Oceanography* **60**, 201–222.

Aller, O.D. 2017. Descripción de la dieta de la medusa *Chrysaora plocamia* (Lesson, 1830) en la bahía Independencia, Perú durante el evento El Niño costero 2017. Universidad Científica del Sur, Lima, Perú, 50 pp.

Aller, O.D. 2018. Descripción de la dieta de la scyphomedusa (*Chrysaora plocamia* (Lesson, 1830) en la bahía Independencia (Pisco, Perú) en un período del evento El Niño Costero 2017). BSc thesis, Universidad Científica del Sur, Lima, Perú, 66 pp.

Antezana, T. 2002. Adaptive behavior of *Euphausia mucronata* in relation to the oxygen minimum layer of the Humboldt Current. *Oceanography of the eastern Pacific* **2**, 29–40.

Arai, M.N. 1997. *A Functional Biology of Scyphozoa*. London: Chapman and Hall.

Arístegui, J., Barton, E.D., Álvarez-Salgado, X.A., Santos, A.M.P., Figueiras, F.G., Kifani, S., Hernández-León, S., Mason, E., Machu, E. & Demarcq, H. 2009. Subregional ecosystem variability in the Canary Current upwelling. *Progress in Oceanography* **83**, 33–48.

Aronés, K., Grados, D., Ayón, P. & Bertrand, A. 2019. Spatio-temporal trends in zooplankton biomass in the northern Humboldt Current System off Peru from 1961–2012. *Deep Sea Research Part II* **169**, 104656.

Atkinson, L.P., Valle-Levinson, A., Figueroa, D., De Pol-Holz, R., Gallardo, V.A., Schneider, W., Blanco, J.L. & Schmidt, M. 2002. Oceanographic observations in Chilean coastal waters between Valdivia and Concepción. *Journal of Geophysical Research Oceans* **107**(C7), 1–13.

Auger, P-A, Machu, R., Gorgues, T., Grima, N. & Waelas, M. 2015. Comparative study of potential transfer of natural and anthropogenic cadmium to plankton communities in the North-West African upwelling. *Science of the Total Environment* **505**, 870–888.

Avian, M., Ramšak, A., Tirelli, V., D'Ambra, I. & Malej, A. 2016. Redescription of *Pelagia benovici* into a new jellyfish genus, *Mawia*, gen. nov., and its phylogenetic position within Pelagiidae (Cnidaria: Scyphozoa: Semaeostomeae). *Invertebrate Systematics* **30**, 523–546.

Ayón, P, Criales-Hernandez, M.I., Schwamborn, R. & Hirche, H.J. 2008. Zooplankton research off Peru: A review. *Progress in Oceanography* **79**(2–4), 238–255.

Bailey, H., S.R. Benson, G.L. Shillinger, S.J. Bograd, P.H. Dutton, S.A. Eckert, S.J. Morreale, F.V. Paladino, T. Eguchi, D.G. Foley, B.A. Block, R. Piedra, C. Hitipeuw, R.F. Tapilatu & Spotila, J.R. 2012. Identification of distinct movement patterns in Pacific leatherback turtle populations influenced by ocean conditions. *Ecological Applications* **22**, 735– 747.

Bakun, A. 1990. Global climate change and intensification of coastal ocean upwelling. *Science* **247**(4939), 198–201.

Bakun, A. 1996. *Patterns in the Ocean: Ocean Processes and Marine Population Dynamics*. La Paz, Mexico: University of California Sea Grant Program, San Diego, California, USA, in cooperation with Centro de Investigaciones Biológicas de Noroeste, 323 pp.

Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. *Progress in Oceanography* **68**, 271–288.

Bakun, A., Black, B.A., Bograd, S.J., García-Reyes, M., Miller, A.J., Rykaczewski, R.R. & Sydeman, W.J. 2015. Anticipated effects of climate change on coastal upwelling ecosystems. *Current Climate Change Reports* **1**, 85–93.

Bakun, A., Field, D.B., Redondo-Rodriguez, A.N.A. & Weeks, S.J. 2010. Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. *Global Change Biology* **16**, 1213–1228.

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

Bakun, A. & Weeks, S. J. 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.

Båmstedt, U., Wild, B. & Martinussen, M.B. 2001. Significance of food type for growth of ephyrae *Aurelia aurita* (Scyphozoa). *Marine Biology* **139**, 641–650.

Barange, M. & Boyd, A.J. 1992. Life history, circulation and maintenance of *Nyctiphanes capensis* (Euphausiacea) in the northern Benguela upwelling system. *South African Journal of Marine Science* **12**(1), 95–106.

Barange, M & Pillar, S.C. 1992. Cross-shelf circulation, zonation and maintenance mechanisms of *Nyctiphanes capensis* and *Euphausia hanseni* (Euphausiacea) in the northern Benguela upwelling system. *Continental Shelf Research* **12**, 1027–1042.

Barange, M., Pillar, S.C., Huse, I. & Hutchings, L. 2005. Vertical migration, catchability and acoustic assessment of semi-pelagic Cape horse mackerel *Trachurustrachurus capensis* in the southern Benguela. *African Journal of Marine Science* **27**(2), 459–469.

Barange, M., Pillar, S.C. & Hutchings, L. 1992. Major pelagic borders of the Benguela upwelling system according to euphausiid species distributions. *South African Journal of Marine Science* **12**, 3–17.

Barber, R. & Smith, R.L. 1981. Coastal upwelling ecosystems. In *Analysis of Marine Ecosystems*, A.R. Longhurst (ed). London: Academic Press, pp. 31–68.

Barton, E.D., Aristegui, J., Tett, P., Canton, M., Garcia-Braun, J., Hernandez-Leon, S., Nykjær, L., Almeda, C., Almunia, J., Ballesteros, S., Basterretxea, G., Escanez, J., Garcia-Weill, L., Hernandez-Guerra, A., Lopez-Laatzen, F., Molina, R., Montero, M.F., Navarro-Perez, E., Rodriguez, J.M., Van Klenning, K., Velez, H. & Wild, K. 1998. The transition zone of the Canary Current upwelling region. *Progress in Oceanography* **41**, 455–504.

Barz, K., Hinrichsen, H.H. & Hirche, H.J. 2006. Scyphozoa in the Bornholm Basin (central Baltic Sea) - The role of advection. *Journal of Marine Systems* **60**, 167–176.

Bayha, K.M., Collins, A.G. & Gaffney, P.M. 2017. Multigene phylogeny of the scyphozoan jellyfish family Pelagiidae reveals that the common U.S. Atlantic sea nettle comprises two distinct species (*Chrysaora quinquecirrha* and *C. chesapeakei*). *PeerJ* **5**, e3863.

Bayha, K.M. & Dawson, M.N. 2010. New family of allomorphic jellyfishes, Drymonematidae (Scyphozoa, Discomedusae), emphasizes evolution in the functional morphology and trophic ecology of gelatinous zooplankton. *Biological Bulletin* **219**(3), 249–267.

Benazzouz, A., Mordane, S., Orbi, A., Chagdali, M., Hilmi, K. & Atillah, A. 2014. An improved coastal upwelling model for climatology and enviroment index from sea surface temperature using satellite-based approach - the case of the Canary Current upwelling system. *Continental Shelf Research* **81**, 38-54.

Benedetti-Cecchi, L., Canepa, A., Fuentes, V., Tamburello, L., Purcell, J.E., Piraino, S., Roberts, J., Boero, F. & Halpin, P. 2015. Deterministic factors overwhelm stochastic environmental fluctuations as drivers of jellyfish outbreaks. *PLoS One* **10**(10), 1–16, e0141060, doi: 10.1371/journal.pone.0141060

Benson, S.R., Eguchi, T., Foley, D.G, Forney, K.A, Bailey, H., Hitipeuw, C., Samber, B.P., Tapilatu, B.P., Rei, V., Ramohia, P., Pita, J. & Dutton P. H. 2011. Large-scale movements and high-use areas of western Pacific leatherback turtles, *Dermochelys coriacea*. *Ecosphere* **2**(7), 1–27.

Benson, S.R., Forney, K.A., Harvey, J.T., Carretta, J.V. & Dutton, P.H. 2007. Abundance, distribution, and habitat of leatherback turtles (*Dermochelys coriacea*) off California, 1990–2003. *Fishery Bulletin* **105**, 337–347.

Bertrand, A., Segura, M., Gutiérrez, M. & Vásquez, L. 2004. From small-scale habitat loopholes to decadal cycles: A habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. *Fish and Fisheries* **5**, 296–316.

Bertrand, A., Vögler, R. & Defeo, O. 2018. Climate change impacts, vulnerabilities and adaptations: Southwest Atlantic and Southeast Pacific marine fisheries. In *Impacts of Climate Change on Fisheries and Aquaculture: Synthesis of Current Knowledge, Adaptation and Mitigation Options*, M. Barange, T. Bahri, M. Beveridge, K. Cochrane, S. Funge-Smith, & F. Poulain et al. (eds). *FAO Fisheries and Aquaculture Technical Paper* **627**, 628 pp.

Binet, D. 1991. Dynamique du plancton dans les eaux côtières ouest-africaines: écosystèmes équilibrés et déséquilibrés. In *Pêcheries ouest-africaines, Variabilité, Instabilité et Changement*. P. Cury & C. Roy (éds). Paris: *ORSTOM*, pp. 117–136.

Bode, M., Kreiner, A., van der Plas, A.K., Louw, D.C., Horaeb, R., Auel, H. & Hagen, W. 2014 Spatio-Temporal variability of copepod abundance along the 20°S monitoring transect in the Northern Benguela Upwelling System from 2005 to 2011. *PLoS One* **9**(5), e97738.

Boero, F. 2013. Review of jellyfish blooms in the Mediterranean and Black Sea. *GFCM Studies and Reviews* **92**, 53 pp.

Boero, F., Bouillon, J., Gravili, C., Miglietta, M.P., Parsons, T. & Piraino, S. 2008. Gelatinous plankton: Irregularities rule the world (sometimes). *Marine Ecology Progress Series* **356**, 299–310.

Boero, F., Brotz, L., Gibbons, M.J., Pirano, S. & Zampardi, S. 2016. Impacts and effects of ocean warming on jellyfish. In *Explaining Ocean Warming: Causes, Scale, Effects and Consequences*. D. Laffoley & J.M. Baxter (eds). Full report. Gland, Switzerland: IUCN, pp. 231–237.

Bouckaert, R., Vaughan, T.G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F.K., Müller, N.F. Ogilvie, H.A., Du Plessis, L., Popinga, A. Rambaut, A., Rasmussen, D., Siveroni, I., Suchard, M.A., Wu, C-H., Xie, D., Zhang, C., Stadler, T. & Drummond, A.J. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* **15**(4), e1006650. Available at: https://beast.community/programs.

Bowen, B.W., Gaither, M.R., DiBattista, J.D., Iacchei, M., Andrews, K.R., Grant, W.S., Toonen, R.J. & Briggs, J.C. 2016. Comparative phylogeography of the ocean planet. *Proceedings of the National Academy of Sciences* **113**, 7962–7969.

Bowen, B. & Grant, W.S. 1997. Phylogeography of the sardines (*Sardinops s*pp.): Assessing biogeographic models and population histories in temperate upwelling zones. *Evolution* **51**(5), 1601–1610.

Boyer, D. 1996. Stock dynamics and ecology of pilchard in the northern Benguela. In *The Benguela Current and Comparable Eastern Boundary Upwelling Ecosystems*, M.J. O'Toole (ed.). Eschborn, Germany: Deutsche Gesellschaft für Techhnische Zusammenarbeit (GTZ) GmbH, pp. 79–82.

Boyer, D.C., Boyer, H.J., 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 fishing and the environment. *South African Journal of Marine Science* **23**, 67–84.

Boyer, D.C. & Hampton, I. 2001. An overview of the living marine resources of Namibia. *South African Journal of Marine Science* **23**(1), 5–35.

Bravo, V., Palma, S. & Silva, N. 2011. Distribución estacional y vertical de medusas en la región de Aysén, sur de Chile. *Latin America Journal of Aquatic Research* **39**, 359–377.

Brierley, A.S., Axelsen, B.E., Boyer, D.C., Lynam, C.P., Didcock, C.A., Boyer, H,J., Sparks, C.A.J., Purcell, J.E. & Gibbons, M.J. 2004. Single-target echo detections of jellyfish. *ICES Journal of Marine Science* **61**, 383–393.

Brierley, A.S., Axelsen, B.E., Buecher, E., Sparks, C., Boyer, H. & Gibbons, M.J. 2001. Acoustic observations of jellyfish in the Namibian Benguela. *Marine Ecology Progress Series* **210**, 55–66.

Brierley, A.S., Boyer, D.C., Axelsen, B.E., Lynam, C.P., Sparks, C.A.J., Boyer, H. & Gibbons, M.J. 2005. Towards the acoustic estimation of jellyfish abundance. *Marine Ecology Progress Series* **295**, 105–111.

Brodeur, R.D., Auth, T.D. & Phillips, A. 2019. Major shifts in pelagic micronekton and macrozooplankton community structure in an upwelling ecosystem related to an unprecedented marine heatwave. *Frontiers in Marine Science* **6**, 212.

Brodeur, R.D., Barceló, C., Robinson, K.L., Daly, E.A. & Ruzicka, J.J. 2014. Spatial overlap between forage fishes and the large medusa Chrysaora fuscescens in the northern California Current region. *Marine Ecology Progress Series* **510**, 167–181.

Brodeur, R.D., Buckley, T.W., Lang, G.M., Draper, D.L., Buchanan, J.C. & Hibpshman R.E. 2021. Demersal fish predators on gelatinous zooplankton in the Northeast Pacific Ocean. *Marine Ecology Progress Series* **658**, 89-104.

Brodeur, R.D., Decker, M-B., Ciannelli, L., Purcell, J.E., Bond, N.A., Stabeno, P.J., Acuna, E. & Hunt Jr, G.L. 2008a. Rise and fall of jellyfish in the eastern Bering Sea in relation to climate regime shifts. *Progress in Oceanography* **77**, 103–111.

Brodeur, R.D., Hunsicker, M.E., Hann, M.E. & Miller, T.W. 2019. Effects of warming ocean conditions on feeding ecology of small pelagic fishes in a coastal upwelling ecosystem: A shift to gelatinous food sources. *Marine Ecology Progress Series* **617–618**, 149–163.

Brodeur, R.D., Link, J.S., Smith, B.E., Ford, M.D., Kobayashi, D.R. & Jones, T.T. 2016. Ecological and economic consequences of ignoring jellyfish: A plea for increased monitoring of ecosystems. *Fisheries* **41**, 630–637.

Brodeur, R.D., Pearcy, W.G. & Ralston, S. 2003. Abundance and distribution patterns of nekton and micronekton in the Northern California Current Transition Zone. *Journal of Oceanography* **59**, 515– 534.

Brodeur, R.D., Ruzicka, J.J. & Steele, J.H. 2011. Investigating alternate trophic pathways through gelatinous zooplankton and planktivorous fishes in an upwelling ecosystem using end-to-end models. In *Interdisciplinary Studies on Environmental Chemistry – Marine Environmental Modeling & Analysis*, K. Omori, K., X. Guo, N. Yoshie, N. Fujii, I. C. Handoh, A. Isobe. & S. Tanabe et al. (eds). Tokyo: TERRAPUB, pp. 57–63.

Brodeur, R.D., Suchman, C.L., Reese, D., Miller, T. & Daly, E. 2008b. Spatial overlap and trophic interactions between fish and large jellyfish in the Northern California Current. *Marine Biology* **154**, 649–659.

Brodeur, R.D., Sugisaki, H. & Hunt, G.L. 2002. Increases in jellyfish biomass in the Bering Sea: Implications for the ecosystem. *Marine Ecology Progress Series* **233**, 89–103.

Brotz, L., Cheung, W.W.L., Kleisner, K., Pakhomov, E. & Pauly, D. 2012. Increasing jellyfish populations: Trends in Large Marine Ecosystems. *Hydrobiologia* **690**, 3–20.

Brown, P.C., Painting, S.J. & Cochrane, K.L. 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, M.J. 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, D.S. 1983. Assessment and management of pelagic stocks in the southern Benguela region. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources*, G.D. Sharp & J. Csirke (eds). Rome: FAO, *FAO Fisheries Report* **291**, pp. 329–405.

Cáceres, I.P. 2012. Analysing the population dynamics of *Chrysaora plocamia* (Lesson 1830) using fisheries models (in Spanish). BSc thesis, Universidad de Antofagasta, Chile, 20 pp.

Cai, W., Santoso, A., Wang, G., Yeh, S.W., An, S.I., Cobb, K.M., Collins, M., Guilyardi, E., Jin, F., Kug, J-S., Lengaigne, M., McPhaden, M.J., Takahashi, K., Timmermann, A., Vecchi, G., Watanabe, M. & Wu, L. 2015. ENSO and greenhouse warming. *Nature Climate Change* **5**(9), 849–859.

Canepa, A., Fuentes, A., Marambio, M., López, L., Deidun, A., Yahia, OK-D., Yahia, N.D., Piraino, S. & Fuentes, V. 2016. Forecasting jellyfish blooms in the Mediterranean Sea: The Med-JellyRisk Project. 5th International Jellyfish Bloom Symposium Barcelona May 30- June 3, JBS-13 / Oral Presentation_04.

Cardona, L., Alvarez de Quevedo, I., Borrell, A. & Aguilar, A. 2012. Massive consumption of gelatinous plankton by mediterranean apex predators. *PLoS One* **7**, e31329. doi:10.1371/journal.pone.0031329.

Carr, M.E. 2001. Estimation of potential productivity in Eastern Boundary Currents using remote sensing. *Deep-Sea Research Part II* **49**, 59–80.

Carré, M., Sachs, J.P., Purca, S., Schauer, A.J., Braconnot, P., Falcón, R.A. & Lavallée, D. 2014. Holocene history of ENSO variance and asymmetry in the eastern tropical Pacific. *Science* **345**(6200), 1045–1048.

Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution* **17**, 540–552.

Ceh, J., Gonzalez, J., Pacheco, A.S. & Riascos, J.M. 2015. The elusive life cycle of scyphozoan jellyfish - metagenesis revisited. *Scientific Reports* **5**, 12037.

Ceh, J. & Riascos, J.M. 2017. Cryptic life stages in scyphozoan jellyfish: Larval settlement preferences of the South American sea nettle *Chrysaora plocamia*. *Journal of Experimental Marine Biology and Ecology* **490**, 52–55.

Chapman, P. & Shannon, L.V. 1985. The Benguela Ecosystem, Part 2. Chemistry and related processes. *Oceanography and Marine Biology: An Annual Review* **23**, 183–251.

Chavez, F.P., Barber, R.T., Kosro, P.M., Huyer, A., Ramp, S.R., Staton, T.P. & Rojas de Mendiola, B. 1991. Horizontal transport and the distribution of nutrients in the coastal transition zone off northen Carlifornia: Effects on primary production, phytoplankton biomass, and species composition. *Journal of Geophysical Research* **96**, 14833–14848.

Chavez, F.P., Bertrand, A., Guevara-Carrasco, R., Soler, P. & Csirke, J. 2008. The northern Humboldt Current system: Brief history, present status and a view towards the future. *Progress in Oceanography* **79**, 95–105.

Chavez, F.P. & Messié, M. 2009. A comparison of eastern boundary upwelling ecosystems. *Progress in Oceanography* **83**(1–4), 80–96.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E. & Niquen, M. 2003. From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. *Science* **299**, 217–221.

Chavez, F.P., Strutton, P.G., Friederich, G.E., Feely, R.A., Feldman, G.C., Foley, D.G. & McPhaden, M.G. 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997–1998 El Niño. *Science* **286**:2126–2131.

Checkley, D., Alheit, J., Oozeki, Y. & Roy, C. 2009. *Climate Change and Small Pelagic Fish*. Cambridge: Cambridge University Press.

Checkley, D.M. & Barth, J.A. 2009. Patterns and processes in the California Current System. *Progress in Oceanography* **83**, 49–64.

Cheung, W.W., Bruggeman, J. & Butenschön, M. 2018. Projected changes in global and national potential marine fisheries catch under climate change scenarios in the twenty-first century. In *Impacts of Climate Change on Fisheries and Aquaculture: Synthesis of Current Knowledge, Adaptation and Mitigation Options*, M. Barange, T. Bahri, M. Beveridge, K. Cochrane, S. Funge-Smith & F. Poulain et al. (eds). *FAO Fisheries and Aquaculture Technical Paper* **627**, 628 pp.

Chiaverano, L.M., Robinson, K.L., Tam, J., Ruzicka, J.J., Quiñones, J., Aleksa, K.T., Hernandez, F.J., Brodeur, R.D., Leaf, R., Uye, S.I., Decker, M.B., Acha, M., Mianzan, H.W. & Graham, W.M. 2018. Evaluating the role of large jellyfish and forage fishes as energy pathways, and their interplay with fisheries, in the Northern Humboldt Current System. *Progress in Oceanography* **164**, 28–36.

Christensen, V. & Pauly, D. 1992. ECOPATH II – A software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling*. **61**, 169–185.

Condon, R.H., Duarte, C.M., Pitt, K.A., Robinson, K.L., Lucas, C.H., Sutherland, K.R., Mianzan, H.W., Bogeberg, M., Purcell, J.E., Decker, M.B., Uye, S-i., Madin, L.P., Brodeur, Haddock, S.H.D., Malej, A., Parry, G.D., Eriksen, E., Quiñones, J., Acha, M., Harvey, M., Arthur, J.M. & Graham, W.M. 2013. Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences* **110**, 1000–1005.

Conley, K.R. 2013. *Settlement preferences of the Pacific sea nettle, Chrysaora fuscescens, and the socioeconomic impacts of jellyfish on fishers in the Northern California Current*. Master's thesis, University of Oregon, Eugene, Oregon, USA.

Conley, K.R. & Sutherland, K.R. 2015. Commercial fishers' perceptions of jellyfish interference in the Northern California Current. *ICES Journal of Marine Science* **72**, 1565–1575.

Crawford, R.J.M. 2007. Food, fishing and seabirds in the Benguela upwelling system. *Journal of Ornithology* **148**, S253–S260.

Crawford, R.J.M., Tree, A.J., Whittington, P.A., Visagie, J., Upfold, L., Roxburg, K.J., Martin, A.P. & Dyer, B.M. 2008. Recent distributional changes of seabirds in South Africa: Is climate having an impact? *African Journal of Marine Science* **30**, 189–193.

Cury, P.M., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J. & Verheye, H.M. 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.M., Boyd, I.L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R.J., Furness, R.W., Mills, J.A., Murphy, E.J., Österblom, H., Paleczny, M., Piatt, J.F. 2011. Global seabird response to forage fish depletion – one-third for the birds. *Science* **334**, 1703–1706.

Cury, P.M. & 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.

Cury, P.M., Shannon, L.J., Roux, J.-P., Daskalov, G.M., Jarre, A., Moloney, C.L. & Pauly, D. 2005. Trophodynamic indicators for an Ecosystem Approach to Fisheries. *ICES Journal of Marine Science* **62**, 430–442.

D'Amato, M.E., Harkins, G.W., deOliveira, T., Teske, P.R. & Gibbons, M.J. 2008. Molecular dating and biogeography of the neritic krill *Nyctiphanes*. *Marine Biology* **155**, 243–247.

D'Ambra, I., Carmichael, R.H. & Graham, W.M. 2014. Determination of δ^{13}C and δ^{15}N and trophic fractionation in jellyfish: Implications for food web ecology. *Marine Biology* **161**, 473–480.

Darriba, D.D., Taboada, G.L.G., Doallo, R.R. & Posada, D.D. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* **9**, 772–772.

Dawson, M.N. 2004. Some implications of molecular phylogenetics for understanding biodiversity in jellyfishes, with emphasis on Scyphozoa. *Hydrobiologia* **530/531**, 249–260.

Decker, M.B., Cieciel, K., Zavolokin, A., Lauth, R., Brodeur, R.D. & Coyle, K.O. 2014. Population fluctuations of jellyfish in the Bering Sea and their ecological role in this productive shelf ecosystem. In *Jellyfish blooms*, K.A. Pitt & C.H. Lucas (eds). Dordrecht: Springer, pp. 153–183.

Demarcq, H. & Benazzouz, A. 2015. Trends in phytoplankton and primary productivity off Northwest Africa. In *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem* Valdés, L. & Déniz-González, I. (eds). Paris: IOC- UNESCO. *IOC Technical Series*, No. **115**, pp. 331–334.

Di Camillo, C.G., Betti, F., Bo, M., Martinelli, M., Puce, S., & Bavestrello, G. 2010. Contribution to the understanding of 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.

Di Lorenzo, E. & Mantua, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change* **6**, 1042–1047.

Duarte, C.M., Pitt, K.A., Lucas, C.H., Purcell, J.E., Uye, S., Robinson, K., Brotz, L., Decker, M.B., Sutherland, K.R., Malej, A., Madin, L., Mianzan, H., Gili, J.-M., Fuentes, V., Atienza, D., Pagés, F., Breitburg, D., Malek, J., Graham, W.M. & Condon, R.H. 2012. Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment* **11**, 91–97.

Dupouy, C., Rébert, J.P. & Touré, D. 1986. Nimbus 7 coastal zone color scanner pictures of phytoplankton growth on an upwelling front in Senegal. In: "*Biological Processes at Marine Physical Interfaces*", Liège colloquium, May 1985, Nihoul (edition), 26 pp.

Eckelbarger, K.J. 1994. Diversity of metazoan ovaries and vitellogenic mechanisms: Implications for life history theory. *Proceedings of the Biological Society of Washington*. **107**(1), 193–218.

Eckelbarger, K.J. & Larson, R.J. 1988. Ovarian morphology and oogenesis in *Aurelia aurita* (Scyphozoa: Semaeostomeae): Ultrastructural evidence of heterosynthetic yolk formation in a primitive metazoan. *Marine Biology* **100**, 103–115.

Elliot, W., Gonzáles, R., Becerra, W. & Ramírez, A. 1999. Biología y pesquería del pampanito pintado Stromateus stellatus Cuvier en la zona de Huacho (Perú) durante enero a setiembre 1999. *Informe Progresivo, Instituto del Mar del Perú (Ene 2000)* **112**, 23 pp.

Emery, W. 2001. Water types and water masses. In *Encyclopedia of Ocean Sciences: Elements of Physical Oceanography*. S.A. Thorpe (ed.). London: Elsevier, pp. 3179–3187.

Escribano, R. 1998. Population dynamics of *Calanus chilensis* in the Chilean Eastern Boundary Humboldt Current. *Fisheries Oceanography* **7**, 245–251.

Escribano, R. & Hidalgo, P. 2000. Influence of El Niño and La Niña on the population dynamics of *Calanus chilensis* in the Humboldt Current ecosystem of northern Chile. *ICES Journal of Marine Science* **57**, 1867–1874.

Espinoza, P. & Bertrand, A. 2008. Revisiting Peruvian anchovy (*Engraulis ringens*) trophodynamics provides a new vision of the Humboldt Current System. *Progress in Oceanography* **79**, 215–227.

Espinoza, P., Bertrand, A., Van der Lingen, C.D., Garrido, S. & De Mendiola, B.R. 2009. Diet of sardine (*Sardinops sagax*) in the northern Humboldt Current system and comparison with the diets of clupeoids in this and other eastern boundary upwelling systems. *Progress in Oceanography* **83**, 242–250.

Fagetti, E. 1973. Medusas de aguas chilenas. *Revista de Biología Marina y Oceanografía* **15**, 31–75.

Fancett, M.S. & Jenkins, G.P. 1988. Predatory impact of scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay. *Journal of Experimental Marine Biology and Ecology* **116**, 63–77.

Fannjiang, C., Mooney, T.A., Cones, S., Mann, D., Shorter, K.A. & Katija, K. 2019. Augmenting biologging with supervised machine learning to study *in situ* behavior of the medusa *Chrysaora fuscescens*. *Journal of Experimental Biology* **222**, 1–10, doi:10.1242/jeb.207654

FAO. 2011. FAO yearbook. Fishery and Aquaculture Statistics. 2011/FAO annuaire. Statistiques des pêches et de l'aquaculture. 2011/FAO anuario. Estadísticas de pesca y acuicultura. 2011. Rome/Roma, FAO. 76 pp.

FAO. 2016. *The State of World Fisheries and Aquaculture 2016 (SOFIA): Contributing to Food Security and Nutrition for All*. Rome: Food and Agriculture Organization, pp. 200.

Fearon, J.J., Boyd, A.J. & Schülein, F.H. 1992 Views on the biomass and distribution of *Chrysaora hysoscella* (Linné, 1766) and *Aequorea aequorea* (Forskål, 1755) off Namibia, 1982–1989. *Scientia Marina* **56**, 75–85.

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

Fernández-Alías, A., Marcos, C., Quispe, J.I., Sabah, S. & Perez-Ruzafa, A. 2020. Population dynamics and growth in three scyphozoan jellyfishes, and their relationship with environmental conditions in a coastal lagoon. *Estuarine, Coastal and Shelf Science* **243**, 106901.

Field, J. C., Francis, R.C. & Aydin, K. 2006. Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current. *Progress in Oceanography* **68**, 238–270.

Figueroa, D. 2002. Forcing of physical exchanges in the nearshore Chilean ocean. In *The Oceanography and Ecology of the Nearshore and Bays in Chile*, J.C. Castilla & J.L. Largier (ed.). Santiago: Ediciones Universidad Católica de Chile, pp. 31–43.

Flament, P., Armi, L. & Washburn, L. 1985. The evolving structure of an upwelling filament. *Journal of Geophysical Research* **90**, 11765–11778.

Florenchie, P., Reason, C.J.C., Lutjeharms, J.R.E., Rouault, M., Roy, C. & Masson, S. 2003. The source of Benguela Ninos in the South Atlantic Ocean. *Geophysical Research Letters* **30**(10), 1505.

Flynn, B.A. & Gibbons, M.J. 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.

Flynn, B.A., Richardson, A.J., Brierley, A.S., Boyer, D.C., Axelsen, B.E., Scott, L., Moroff, N.E., Kainge, P.I., Tjizoo, B.M. & Gibbons, M.J. 2012. Temporal and spatial patterns in the abundance of jellyfish in the northern Benguela upwelling ecosystem and their link to thwarted pelagic fish recovery. *African Journal of Marine Science* **34**, 131–146.

Fossette, S., Katija, K., Goldbogen, J., Bograd, S., Patry, W., Howard, M., Knowles, T., Haddock, S., Bedell, L., Hazen, E., Robison, B., Mooney, T., Shorter, K., Bastian, T. & Gleiss, A. 2016. How to tag a jellyfish? A methodological review and guidelines to successful jellyfish tagging. *Journal of Plankton Research* **38**, 1347–1363.

Fréon, P., Arístegui, J., Bertrand, A., Crawford, R.J.M., Field, J.C., Gibbons, M.J., Tam, J., Hutchings, L., Masski, H., Mullon, C., Ramdani, M., Seret, B. & Simier, M. 2009. Functional group biodiversity in Eastern Boundary Upwelling Ecosystems questions the wasp-waist trophic structure. *Progress in Oceanography* **83**, 97–106.

Fréon, P., Bouchon, M., Mullon, C., García, C. & Ñiquen, M. 2008. Interdecadal variability of anchoveta abundance and overcapacity of the fishery in Peru. *Progress in Oceanography* **79**, 401–412.

Freund, M.B., Henley, B.J., Karoly, D.J., McGregor, H.V., Abram, N.J. & Dommenget, D. 2019. Higher frequency of Central Pacific El Niño events in recent decades relative to past centuries. *Nature Geoscience* **12**, 450–455.

Furnestin, M.L. 1957. Chaetognathes et zooplancton du secteur atlantique marocain. *Revue des Travaux de l'Institut des Peches Maritimes* **21**, 356 pp.

Furnestin, M.L. 1959. Méduses du plancton marocain. *Revue des Travaux de l'Institut des Pêches Maritimes (0035–2276) (ISTPM)* **23**(1), 105–124.

Furnestin, M.L. 1976. Les copépodes du plateau continental marocain et du détroit canarien. I. Répartition quantitative. *Conseil Permanent International pour l'Exploration de la Mer* **8**, 22–46.

Galigher, A.E. 1925. On the occurrence of the larval stages of Scyphozoa in the Elkhorn Slough, Monterey Bay, California. *The American Naturalist* **59**(660), 94–96.

Gallo, N.D., Drenkard, E., Thompson, A.R., Weber, E.D., Wilson-Vandenberg, D., McClatchie, S., Koslow, J.A. & Semmens, B.X. 2019. Bridging from monitoring to solutions-based thinking: Lessons from calcofi for understanding and adapting to marine climate change impacts. *Frontiers in Marine Science* **6**, 695, doi:10.3389/fmars.2019.00695

Ganoza, F., Castillo, P.R. & Marín, D. 2000. Variaciones estacionales en la distribución y biomasa de anchoveta entre 1983 y 2000. *Boletín del Instituto del Mar del Perú* **19**, 157–177.

García-Reyes, M., Sydeman, W.J., Schoeman, D.S., Rykaczewski, R.R., Black, B.A., Smit, A.J. & Bograd, S.J. 2015. Under pressure: Climate change, upwelling, and Eastern Boundary Upwelling Ecosystems. *Frontiers In Marine Science* **2**, 109.

Gasca, R. & Haddock, S.H. 2004. Associations between gelatinous zooplankton and hyperiid amphipods (Crustacea: Peracarida) in the Gulf of California. *Hydrobiologia* **530**(1–3), 529–535.

Gershwin, L-A. 2001. Systematics and biogeography of the jellyfish *Aurelia labiata* (Cnidaria: Scyphozoa). *The Biological Bulletin* **201**(1), 104–119.

Gershwin, L. & Collins, A.G. 2002. A preliminary phylogeny of Pelagiidae (Cnidaria, Scyphozoa), with new observations of Chrysaora colorata comb. nov. *Journal of Natural History* **36**, 127–148.

Gibbons, M.J., Boero, F. & Brotz, L. 2015. We should not assume that fishing jellyfish will solve our jellyfish problem. *ICES Journal of Marine Science* **73**, 1012–1018.

Gibbons, M.J., Buecher, E. & Thibault-Botha, D. 2003. Observations on the ecology of *Pleurobrachia pileus* (Ctenophora) in the southern Benguela ecosystem. *South African Journal of Marine Science* **25**, 253–261.

Gibbons, M.J. & Hutchings, L. 1996. Zooplankton diversity and community structure around southern Africa, with special attention to the Benguela upwelling system. *South African Journal of Science* **92**, 63–76.

Gibbons, M.J. & Richardson, A.J. 2013. Beyond the jellyfish joyride and global oscillations: Advancing jellyfish research. *Journal of Plankton Research* **35**, 929–938.

Gibson, G.A., & Spitz, Y.H. 2011. Impacts of biological parameterization, initial conditions, and environmental forcing on parameter sensitivity and uncertainty in a marine ecosystem model for the Bering Sea. *Journal of Marine Systems* **88**, 214–231.

Giribet, G. & Edgecombe, G.D. 2020. *The Invertebrate Tree of Life*. Princeton, New Jersey: Princeton University Press, 590 pp.

Glessmer, M.S., Carsten, E. & Andreas, O. 2009. Contribution of oxygen minimum zone waters to the coastal upwelling off Mauritania. *Progress in Oceanography* **83** (1–4), 143–150, doi:10.1016/j.pocean.2009.07.015

Gomez Daglio, L. & Dawson, M.N. 2017. Species richness of jellyfishes (Scyphozoa: Discomedusae) in the Tropical Eastern Pacific: Missed taxa, molecules, and morphology match in a biodiversity hotspot. *Invertebrate Systematics* **31**, 635–663.

Gordon, M. & Seymour, J. 2012. Growth, development and temporal variation in the onset of six *Chironex fleckeri* medusae seasons: A contribution to understanding jellyfish ecology. *PLoS One* **7**, e31277.

Goya, E., Quiñones, J. & de Paz, N. 2011. *Informe Nacional sobre la Situación de las Tortugas Marinas en el Perú*. Lima: Comisión Permanente del Pacifico Sur (CPPS).

Graham, T.R., Harvey, J.T., Benson, S.R., Renfree, J.S. & Demer, D.A. 2010. The acoustic identification and enumeration of Scyphozoan jellyfish, prey for leatherback sea turtles (*Dermochelys coriacea*), off central California. *ICES Journal of Marine Science* **67**(8), 1739–1748.

Graham, W.M. 1994. *The physical oceanography and ecology of upwelling shadows*. PhD thesis, University of California, Santa Cruz.

Graham, W.M., Field, J.G. & Potts, D.C. 1992. Persistent "upwelling shadows" and their influence on zooplankton distributions. *Marine Biology* **114**(4), 561–570.

Graham, W.M., Gelcich, S., Robinson, K.L., Duarte, C.M., Brotz, L., Purcell, J.E., Madin, L.P., Mianzan, H., Sutherland, K.R., Uye, S., Pitt, K.A., Lucas, C.H., Bøgeberg, M., Brodeur, R.D. & Condon, R.H. 2014. Linking human well-being and jellyfish: Ecosystem services, impacts, and societal responses. *Frontiers in Ecology and the Environment* **12**, 515–523.

Graham, W.M. & Largier, J.L. 1997. Upwelling shadows as nearshore retention sites: The example of northern Monterey Bay. *Continental Shelf Research* **17**(5), 509–532.

Graham, W.M., Pages, F. & Hamner, W.M. 2001. A physical context for gelatinous zooplankton aggregations: A review. In J*ellyfish Blooms: Ecological and Societal Importance*, J.E. Purcell, W.M. Graham & H.J. Dumont (eds). Netherlands: Springer, pp. 199–212.

Grall, J.R., Laborde, P., Le Corre, P., Nerveux, J., Treguer, P. & Thiriot, A. 1974. Caractéristiques trophiques et production planctonique dans la région sud de l'Atlantique marocain. Résultats des campagnes CINECA-CHARCOT I et II. *Téthys* **6** (1–12), 11–28.

Grall, J.R., Le Corre, P. & Tréguer, P. 1982. Short-term variability of primary production in coastal upwelling of Morocco. *Rapports et procès-verbaux des réunions - Commission internationale pour l'exploration scientifique de la mer Méditerranée* **180**, 221–227.

Grant, W.S., Leslie, R.W. & Bowen, B.W. 2005. Molecular genetic assessment of bipolarity in the anchovy genus *Engraulis*. *Journal of Fish Biology* **67**(5), 1242–1265.

Grantham, B.A., Chan, F., Nielsen, K.J., Fox, D.S., Barth, J.A., Huyer, A., Lubchenco, J. & Menge, B.A. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* **429**, 749–754.

Greene, G., Kuehne, L., Rice, C., Fresh, K. & Penttila, D. 2015. Forty years of change in forage fish and jellyfish abundance across greater Puget Sound, Washington (USA): Anthropogenic and climate associations. *Marine Ecology Progress Series* **525**, 153–170.

Griffin, D.C., Harrod, C., Houghton, J.D.R. & Capellini, I. 2019. Unravelling the macro-evolutionary ecology of fish–jellyfish associations: Life in the 'gingerbread house'. *Proceedings of the Royal Society B*. **286**, 9 pp.

Guindon, S., Dufayard, J-F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O. 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Systematic Biology* **59**(3), 307–321.

Gutiérrez, D., Akester, M. & Naranjo, L. 2016. Productivity and sustainable management of the Humboldt Current large marine ecosystem under climate change. *Environmental Development* **17**, 126–144.

Gutiérrez, D., Sifeddine, A., Field, D.B., Ortlieb, L., Vargas, G., Chaávez, F.P., Velazco, F., Ferreira, V. Tapia, P., Salvatteci, R., Boucher, H., Morales, M.C., Valdés, J., Reyss, J.-L., Campusano, A., Boussafir, M., Mandeng-Yogo, M., García, M. & Baumgartner, T. 2009. Rapid reorganization in ocean biogeochemistry off Peru towards the end of the Little Ice Age. *Biogeosciences* **6**, 835–848.

Hagen, E. 2001. Northwest African upwelling scenario. *Oceanologica Acta* **24**(Suppl.), 113–128.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson, R. 2008. A global map of human impact on marine ecosystems. *Science* **319**(5865), 948–952.

Hansson, L.J., Moeslund, O., Kiørboe, T. & Riisgård, H.U. 2005. Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). *Marine Ecology Progress Series* **304**, 117–131.

Harding, J.A., Ammann, A.J. & MacFarlane, R.B. 2011. Regional and seasonal patterns of epipelagic fish assemblages from the central California Current. *Fishery Bulletin* **109**, 261–281.

Hare, S.R. & Mantua, N.J. 2000. Empirical indicators for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* **47**(2–4), 103–146.

Hart, T.J. & Currie, R.I. 1960. The Benguela Current. *Discoveries Reports* **31**, 123–298.

Häussermann, V., Dawson, M.N. & Försterra, G. 2009. First record of the moon jellyfish, *Aurelia* for Chile. *Spixiana* **32**, 3–7.

Hays, G.C., Doyle, T.K. & Houghton, J.D.R. 2018. A paradigm shift in the trophic importance of jellyfish? *Trends in Ecology and Evolution* **33**, 874–884.

Hays, G.C., Farquhar, M.R., Luschi, P., Teo, S.L., & Thys, T.M. 2009. Vertical niche overlap by two ocean giants with similar diets: Ocean sunfish and leatherback turtles. *Journal of Experimental Marine Biology and Ecology* **370**(1–2), 134–143.

Healey, A.J.E., Farthing, M.W., Nunoo, F.K.E., Potts, W.M., Sauer, W.H.H., Skujina, I., King, N., de Becquevort, S. & Shaw, P.W. 2020. Genetic analysis provides insights into species distribution and population structure in East Atlantic horse mackerel (*Trachurus trachurus* and *T. capensis*). *Journal of Fish Biology* **96**, 795–805.

Heins, A., Sötje, I. & Holst, S. 2018. Assessment of investigation techniques for scyphozoan statoliths, with focus on early development of the jellyfish *Sanderia malayensis*. *Marine Ecology Progress Series* **591**, 37–56.

Heitstuman, T.M. 1994. *Aspects of the biology and culture of Scyphomedusae of the Oregon coast*. Master's thesis, Oregon State University, Corvallis, Oregon, USA.

Hellberg, M.E. 1996. Dependence of gene flow on geographic distance in two solitary corals with different larval dispersal capabilities. *Evolution* **50**, 1167–1175.

Helm, R.R. 2018. Evolution and development of scyphozoan jellyfish. *Biological Reviews* **93**, 1228–1250.

Helm, R.R. & Gibbons, M.J. 2008. Planktic cnidaria along the South and Southwest coast of South Africa – mesoscale coupling with the physical environment. Unpublished poster, *Southern African Marine Sciences Symposium*.

Hetherington, E.D., Kurle, C.M., Benson, S.R., Jones, T.T. & Seminoff, J.A. 2019. Re-examining trophic dead ends: Stable isotope values link gelatinous zooplankton to leatherback turtles in the California Current. *Marine Ecology Progress Series* **632**, 205–219.

Heymans, J.J. 1996. *Network analysis of the carbon flow model of the northern Benguela ecosystem, Namibia*. PhD thesis, Faculty of Science, University of Port Elizabeth.

Heymans, J.J. & Baird, D. 2000a. A carbon flow model and network analysis in the northern Benguela upwelling system, Namibia. *Ecological Modelling* **126**, 9–32.

Heymans, J.J. & Baird, D. 2000b. Network analysis of the northern Benguela ecosystem by means of NETWRK and ECOPATH. *Ecological Modelling* **131**, 97–119.

Heymans, J.J., Shannon, L.J. & Jarre, A. 2004. Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s and 1990s. *Ecological Modelling* **172**, 175–195.

Hickey, B.M. 1998. Coastal oceanography of western North America from the tip of Baja California to Vancouver Island. In *The Sea*, Volume 11, A.R. Robinson & K.H. Brink (eds). Wiley & Sons, Inc., pp. 345–393.

Hidalgo, P. & Escribano, R. 2001. Succession of pelagic copepod species in coastal waters off northern Chile: The influence of the 1997–1998 El Niño. *Hydrobiologia* **453**, 153–160.

Hidalgo, P., Escribano, R. & Morales, C.E. 2005. Ontogenetic vertical distribution and diel migration of the copepod *Eucalanus inermis* in the oxygen minimum zone off northern Chile (20–21°S). *Journal of Plankton Research* **27**, 519–529.

Höring, F., Cornils, A., Auel, H., Bode, M. & Held, C. 2017. Population genetic structure of *Calanoides natalis* (Copepoda, Calanoida) in the eastern Atlantic Ocean and Benguela upwelling system. *Journal of Plankton Research* **39**, 618–630.

Hu, X., Wang, J., An, W., Garzanti, E. & Li, J. 2017. Constraining the timing of the India-Asia continental collision by the sedimentary record. *Science China Earth Sciences* **60**, 603–625, doi:10.1007/s11430-016-9003-6

Hughes, P. & Barton, E. 1974. Stratification and water mass structure in the upwelling area off northwest Africa in April/May 1969. *Deep Sea Research* **21**, 611–628.

Hutchings, L., Pillar, S.C. & Verheye, H.M. 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.

Hutchings, L., van der Lingen, C.D., Shannon, L.J., Crawford, R.J.M., Verheye, H.M.S., Bartholomae, CH, van der Plas, A.K., Louw, D., Kreiner, A., Ostrowski, M., Fidelg, Q., Barlow, R.G., Lamontah, T., Coetzee, J., Shillington, F., Veitchh, J., Currie, J.C. & Monteiro, P.M.S. 2009. The Benguela Current: An ecosystem of four components. *Progress in Oceanography* **83**, 15–32.

Idrissi, H.F. 2020. Observations in situ of gelatinous taxa from the deep-sea by using submersibles and remotely-operated vehicles (VAMS). In *INRH internal report* "*Cartography of marine habitats*".

Idrissi, H.F., Charouki, N., Serghini, M. & Ettahiri, O. 2018a. Exploration du lien entre l'abondance du macroplancton gélatineux et quelques variables hydrologiques, du cap Cantin au cap Blanc. Chapter 7.4. *Rapport Baselien CCLME 2018*, p. 14.

Idrissi, H.F., Kifani, S., Kalmouni, A., Chfiri, H. & Charouki, N. 2018b. Spatial occurrence and biodiversity of jellyfish in the Moroccan Atlantic ecosystem between (35°N) and (21°N). Poster. *Preface International Conference on Ocean, Climate ans Ecosystems and Preface Final Assembly Arrecife, Lanzarote (Canary Island, Spain)*, 17–20 April 2018.

Iitembu, J.A., Miller, T.W., Ohmori, K., Kanime, A. & Wells, S. 2012. Comparison of ontogenetic trophic shift in two hake species, *Merluccius capensis* and *Merluccius paradoxus*, from the Northern Benguela Current ecosystem (Namibia) using stable isotope analysis. *Fisheries Oceanography* **21**(2–3), 215–225.

Inejih, C.A., Taleb Sidi, M.O., Diadhiou, H.D. 2014. Assessment of the state of marine biodiversity in the region of the CCLME. Study report. FAO, Rome 1–147. http://www.fao.org/3/a-br707e.pdf.

Irigoien, X. & De Roos, A. 2011. The role of intraguild predation in the population dynamics of small pelagic fish. *Marine Biology* **158**, 1683–1690.

James, A.G. & Findlay, K.P. 1989. Effect of particle size and concentration on feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy *Engraulis capensis*. *Marine Ecology Progress Series* **50**(3), 275–294.

Jarms, G. & Morandini, A.C. 2019. *A World Atlas of Jellyfish. Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, Special Edition, English Edition. Hamburg: Dölling und Galitz Verlag.

Jarre, A. & Pauly, D. 1993. Seasonal changes in the Peruvian upwelling ecosystem. In *Trophic Models of Aquatic Ecosystems*, V. Christensen & D. Pauly (eds). Rome: FAO, *ICLARM Conference Proceedings* **26**, 307–331.

Jarre-Teichmann, A., Shannon, L.J., Moloney, C.L. & Wickens, P.A. 1998. Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. *South African Journal of Marine Science* **19**, 391–414.

Johnson, D.R., Perry, H.M. & Burke, W.D. 2001. Developing jellyfish strategy hypotheses using circulation models. *Hydrobiologia* **451**, 213–321.

Jones, B.H., Mooers, C.N.K., Rienecker, M.M., Stanton, T. & Washburn, L. 1991. Chemical and biological structure and transport of a cool filament associated with a jet-eddy system off northern California in July 1986 (OPTOMA 21). *Journal of Geophysical Research* **96**(12), 2207–2225.

Jones, T.T., Bostrom, B.L., Hastings, M.D., Van Houtan, K.S., Pauly, D. & Jones, D.R. 2012. Resource requirements of the Pacific leatherback turtle population. *PLOS One* **7**, e45447.

Kadila, H.K., Nakwaya, D.N., Butler, M. & Iitembu, J.A. 2020. Insights into feeding interactions of shallow water cape hake (*Merluccius capensis*) and cape horse mackerel (*Trachurus capensis*) from the Northern Benguela (Namibia). *Regional Studies in Marine Science* **34**, 101071.

Kamykowski, D. 2012. 20th century variability of Atlantic meridional overturning circulation: Planetary wave influences on world ocean surface phosphate utilization and synchrony of small pelagic fisheries. *Deep-Sea Research Part I* **65**, 85–99.

Kayal, E., Roure, B., Philippe, H., Collins, A.G. & Lavrov, D.V. 2013. Cnidarian phylogenetic relationships as revealed by mitogenomics. *BMC Evolutionary Biology* **13**, 5.

Kienberger, K. & Prieto, L. 2018. The jellyfish *Rhizostoma luteum* (Quoy & Gaimard, 1827): Not such a rare species after all. *Marine Biodiversity* **48**, 1455–1462.

Kiladis, G.N. 1998. Observations of Rossby waves linked to convection over the eastern tropical Pacific. *Journal of Atmospheric Sciences* **55**, 321–339.

Kim, D.H., Seo, J.N., Yoon, W.D. & Suh, Y.S. 2012. Estimating the economic damage caused by jellyfish to fisheries in Korea. *Fisheries Science* **78**, 1147–1152.

Kramp, P.L. 1952. Medusae collected by the Lund University Chile Expedition 1948–49. Reports of the Lund University Chile Expedition 1948–49. Lunds Universitets Arsskrift, NF, Avd. 2, **47**, 1–19.

Kramp, P.L. 1957. *Hydromedusae from the Discovery Collections. Discovery Report* **29**, 1–128. University Press.

Kramp, P.L. 1965. The Hydromedusae of the Pacific and Indian Oceans. *Dana Report* **63**, 1–162.

Kramp, P.L. 1966. A collection of Medusae from the coast of Chile. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn* **129**, 1–38.

Kramp, P.L. 1968. The Hydromedusae of the Pacific and Indian Oceans. Sections II and III. *Dana Report* **72**, 1–200.

Kudela, R.M., Banas, N.S., Barth, J.A., Frame, E.R., Jay, D.A., Largier, J.L., Lessard, E.J., Peterson, T.D. & Woude, A.J.V. 2008. New insights into the controls and mechanisms of plankton productivity in coastal upwelling waters of the northern California Current System. *Oceanography* **21**, 46– 59.

Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* **35**, 1547–1549.

Laidig, T.E., Adams, P.B. & Samiere, W.M. 1997. Feeding habits of sablefish, Anoplopoma fimbria, off the coast of Oregon and California. In *Biology and Management of Sablefish, Anoplopma Fimbria*, M.E. Wilkins & M.W. Saunders (eds). *NOAA Technical Report* NMFS **130**.

Lamb, P.D., Hunter, E., Pinnegar, J.K., Creer, S., Davies, R.G. & Taylor M.I. 2017 Jellyfish on the menu: mtDNA assay reveals scyphozoan predation in the Irish Sea. *Royal Society open science* **4**, 171421, doi:10.1098/rsos.171421

Lamb, P.D., Hunter, E., Pinnegar, J.K., Doyle, T.K., Creer, S. & Taylor, M.I. 2019. Inclusion of jellyfish in 30+ years of Ecopath with Ecosim models. *ICES Journal of Marine Science* **76**, 1941–1950.

Landry, M.R., Postel, J.R., Peterson, W.K. & Newman, J. 1989. Broad-scale distributional patterns of hydrographic variables on the Washington/Oregon shelf. In *Coastal Oceanography of Washington and Oregon*, M.R. Landry & B.M. Hickey (eds). Amsterdam: Elsevier, pp. 1–40.

Largier, J.L., Lawrence, C.A., Roughan, M., Kaplan, D.M., Dever, E.P., Dorman, C.E., Kudela, R.M., Bollens, S.M., Wilkerson, F.P., Dugdale, R.C., Botsford, L.W., Garfield, N., Kuebel Cervantes, B. & Koračin, D. 2006. WEST: A northern California study of the role of wind-driven transport in the productivity of coastal plankton communities. *Deep-Sea Research II* **53**, 2833–2849.

Larson, R.J. 1986. Ova production by hydromedusae from the NE Pacific. *Journal of Plankton Research* **8**, 995–1002.

Laval, P. 1980 Hyperiid amphipods as crustacean parasitoids associated with gelatinous zooplankton. *Oceanography and Marine Biology Annual Review* **18**, 11–56.

Le Borgne, R. 1983. Note sur les proliférations de Thaliacés dans le golfe de Guinée. *Tropical Oceanography* **18** (1), 49–54.

Lee, Y.W. & Sampson, D.B. 2009. Dietary variations in three co-occurring rockfish species off the Pacific Northwest during anomalous oceanographic events in 1998 and 1999. *Fishery Bulletin* **107**, 510–522.

Lenarz, W.H., Schwing, F.B., VenTresca, D.A., Chavez, F. & Graham, W.M. 1995. Explorations of El Niño events and associated population dynamics off central California. *California Cooperative Oceanic Fisheries Investigations Report* **36**, 106–119.

Levin, L.A. 2018. Manifestation, drivers, and emergence of open ocean deoxygenation. *Annual Review of Marine Science* **10**, 229–260, doi:10.1146/annurev-marine–121916–063359

Louw, D.C., van der Plas, A.K., Mohrholz, V., Wasmund, N., Junker, T. & Eggert, A. 2016. Seasonal and interannual phytoplankton dynamics and forcing mechanisms in the Northern Benguela upwelling system. *Journal of Marine Systems* **157**, 124–134.

Lucas, C.H. & Dawson, M.N. 2014. What are jellyfishes and Thaliaceans and why do they bloom? In *Jellyfish Blooms*, K. Pitt & C. Lucas (eds). Dordrecht: Springer, 9–44.

Lucas, C.H., Graham, W.M. & Widmer, C. 2012. Jellyfish life histories: Role of polyps in forming and maintaining Scyphomedusa populations. *Advances in Marine Biology* **63**, 134–184.

Luo, J.Y., Condon, R.H., Stock, C.A., Duarte, C.M., Lucas, C.H., Pitt, K.A. & Cowen, R.K., 2020. Gelatinous Zooplankton-mediated carbon flows in the global oceans: A data-driven modeling Study. *Global Biogeochemical Cycles* **34**(9), 23 pp. e2020GB006704

Lutjeharms, J.R.E. 2006. *The Agulhas Current*. Berlin Heidelberg: Springer-Verlag, 329 pp.

Lynam, C.P., Gibbons, M.J., Axelsen, B.A., Sparks, C.A.J., Coetzee, J., Heywood, B.G. & Brierley, A.S. 2006. Jellyfish overtake fish in a heavily fished ecosystem. *Current Biology* **16**, 492–493.

Lynam, C.P., Hay, S.J. & Brierley, A.S. 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnology and Oceanography* **49**, 637–643.

Macdonald, P.D.M. & Pitcher, T.J. 1979. Age-groups from size-frequency data: A versatile and efficient method of analyzing distribution mixtures. *Journal of the Fisheries Research Board of Canada* **36**, 987–1001.

Makaoui, A., Orbi, A., Hilmi, K., Zizah, S., Larissi, J. & Talbi, M. 2005. L'upwelling de la côte Atlantique du Maroc entre 1994 et 1998. *Comptes Rendus Geoscience* **337**, 1518–1524.

Malej, A., Vodopivec, M., Lučić, D., Onofri, I. & Pestorić, B. 2014. The lesser-known medusa *Drymonema dalmatinum* Haeckel 1880 (Scyphozoa, Discomedusae) in the Adriatic Sea. *Annals for Istrian and Mediterranean Studies, Series historia naturalis* **24**, 79–86.

Mansueti, R. 1963. Symbiotic behavior between small fishes and jellyfishes, with new data on that between the stromateid, *Peprilus alepidotus*, and the scyphomedusa, *Chrysaora quinquecirrha*. *Copeia* **1963**(1), 40–80.

Marchesiello, P., McWilliams, J.C. & Shchepetkin, A. 2003. Equilibrium structure and dynamics of the California current system. *Journal of Physical Oceanography* **33**, 753–783.

Marín, V.H., Espinoza, S. & Fleminger, A. 1994. Morphometric study of *Calanus chilensis* males along the Chilean coast. *Hydrobiologia* **293**, 75–80.

Marques, M., Darnaude, A.M., Crochemore, S., Bouvier, C. & Bonnet, D. 2019. Molecular approach indicates consumption of jellyfish by commercially important fish species in a coastal Mediterranean lagoon. *Marine Environmental Research* **152**, 104787.

Martin, B., Koppelmann, R., & Kassatovj, P. 2017. Ecological relevance of salps and doliolids in the northern Benguela Upwelling System. *Journal of Plankton Research* **39**, 290–304.

Mauchline, J. 1998. The biology of calanoid copepods. *Advances in Marine Biology* **33**, 1–710.

McClatchie, S. 2014. *Regional Fisheries Oceanography of the California Current System*. Dordrecht: Springer Science, 235 pp.

McGillicuddy, Jr D., Robinson, A., Siegel, D., Jannasch, H., Johnsonk, R., Dickey, T., McNeil, J., Michaels, A.F. & Knap, A. H. 1998. Influence of mesoscale eddies on new production in the Sargasso Sea. *Nature* **394**, 263–266.

Mereghetti, M. 2017. Sardine catches in Namibia, South Africa drop, horse-mackerel stable. *Undercurrent News*. https://www.undercurrentnews.com/2017/03/21/sardine-catches-in-namibia-and-south-africa-drop-horse-mackerel-stable/ (accessed 25 September, 2019).

Mianzan, H.W. 1989. Las medusas Scyphozoa de la Bahía Blanca, Argentina. *Boletim do Instituto Oceanografico* **37**, 29–32.

Mianzan, H.W., Quiñones, J., Palma, S., Schiariti, A., Acha, E.M., Robinson, K.L. & Graham, W.M. 2014. *Chrysaora plocamia*: A poorly understood jellyfish from South American waters. In *Jellyfish Blooms*, K.A. Pitt & C.H. Lucas (eds). Dordrecht, the Netherlands: Springer, pp. 219–236.

Milisenda, G., Martinez-Quintana, A., Fuentes, V.L., Bosch-Belmar, M., Aglieri, G., Boero, F. & Piraino, S. 2018. Reproductive and bloom patterns of *Pelagia noctiluca* in the Strait of Messina, Italy. *Estuarine, Coastal and Shelf Science* **201**, 29–39.

Miller, B.J., von der Heyden, S. & Gibbons, M.J. 2012. Significant population genetic structuring of the holoplanktic scyphozoan *Pelagia noctiluca* in the Atlantic Ocean. *African Journal of Marine Science* **34**, 425–430.

Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop*, pp. 1–8. Available at http://www.phylo.org/.

Miller, R.R., Santora, J.A., Auth, T.D., Sakuma, K.M., Wells, B.K., Field, J.C. & Brodeur, R.D. 2019. Distribution of pelagic Thaliaceans, *Thetys vagina* and *Pyrosoma atlanticum*, during a period of mass occurrence within the California Current. *California Cooperative Oceanic and Fisheries Investegations Reports* **60**, 94–108.

Miller, T.W., Brodeur, R.D., & Rau, G.H. 2008. Carbon stable isotopes reveal relative contribution of shelf-slope production to the northern California Current pelagic community. *Limnology and Oceanography* **53**, 1493–1503.

Mills, C.E. 2001. Jellyfish blooms: Are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* **451**, 55–68.

Mills, C.E. & Larson, R.J. 2007. Scyphozoa: Scyphomedusae, Stauromedusae, and Cubomedusae. In: *Light and Smith's Manual: Intertidal Invertebrates of the Central California Coast*, J.T. Carlton (eds). Berkeley: University of California Press, Fourth Edition, pp. 168–173.

Mills, C.E. & Rees, J.T. 2007. Hydromedusae. In: *Light and Smith's Manual: Intertidal Invertebrates of the Central California Coast*, J.T. Carlton. (ed.). Berkeley: University of California Press, Fourth Edition, pp. 137–168.

Mohamed, M.R., Skrypzeck, H., & Gibbons, M.J. 2019. Describing gonad development and gametogenesis in southern Africa's endemic box jellyfish *Carybdea branchi* (Cubozoa, Carybdeidae). *African Journal of Marine Science* **41**, 83–91.

Möller, H. 1984. Reduction of larval herring populations by jellyfish predation. *Science* **224**, 621–622.

Moloney, C.L., Jarre, A., Arancibia, H., Bozec, Y.M., Neira, S., Roux, J.P. & Shannon, L.J. 2005. Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. *ICES Journal of Marine Science* **62**, 493–502.

Moloney, C.L. Jarre, A., Kimura, S., Mackas, D.L, Maury, O., Murphy, E.J., Peterson, W.T., Runge, J.A. & Tadokoro, K. 2010. Dynamics of marine ecosystems: Ecological processes. In *Marine Ecosystems and Global Change*, M. Barange, J.G. Field, R.P. Harris, E.E. Hofmann, I.R. Perry & F. Werner et al. (eds). England, Oxford: Oxford Press, pp. 179–219.

Monteiro, P.M.S. & van der Plas, A.K., 2006. Low oxygen water (LOW) variability in the Benguela System: Key processes and forcing scales relevant to forecasting. In: *Benguela: Predicting a Large Marine Ecosystem. Large Marine Ecosystems*, volume **14**, V. Shannon, G. Hempel, P. Malanotte-Rizzoli, C.L Moloney & J. Woods. et al. (eds). Amsterdam: Elsevier, pp. 71–90.

Morales, R.M.D.C., Cerpa, C.L.M., Cornejo, S.T.D.R., Girón, C.I.Z., Chacaltana, B.C.A. & Valdivia, V.W. 2020. Geología de la plataforma continental del Perú: paralelos 03° 30´ y 14° 00´ latitud sur. *Boletín del Instituto Geológico, Minero y Metalúrgico Serie D: Estudios Regionales* **32**, 1–118.

Morandini, A.C. & Marques, A.C. 2010. Revision of the genus *Chrysaora* Péron & Lesuer, 1810 (Cnidaria: Scyphozoa). *Zootaxa* **2464** (1), 1–97, doi:10.11646/zootaxa.2464.1.1

Morandini, A.C., Quiñones, J., Stampar, S.N., Cunha, P.R. & Mianzan, H.W. 2013. The metagenetic life cycle of the blooming jellyfish species *Chrysaora plocamia* (Scyphozoa, Pelagiidae). In *Fourth International Jellyfish Blooms Symposium*, Hiroshima.

Morgan, C.A., Beckman, B.R., Weitkamp, L.A., & Fresh, K.L. 2019. Recent ecosystem disturbance in the Northern California Current. *Fisheries* **44**, 465–474.

Mutlu, E., Çağatay, T., Olguner, M.T. & Yilmaz, H.E. 2020. New sea-nettle from the Eastern Mediterranean Sea: *Chrysaora pseudoocellata* sp. nov. (Scyphozoa: Pelagiidae). *Zootaxa* **4790**, 229–244.

Naman, S.M., Greene, C.M., Rice, C.A., Chamberlin, J., Conway-Cranos, L., Cordell, J.R., Hall, J.A. & Rhodes, L.D. 2016. Stable isotope-based trophic structure of pelagic fish and jellyfish across natural and anthropogenic landscape gradients in a fjord estuary. *Ecology and Evolution* **6**, 8159–8173.

Neira, S. & Arancibia, H. 2004. Trophic interactions and community structure in the upwelling system off Central Chile (33–39°S). *Journal of Experimental Marine Biology and Ecology.* **312**, 349–366.

Neira, S., Moloney, C., Christensen, V., Cury, P., Shannon, L. & Arancibia, H. 2014. Analysing changes in the southern Humboldt ecosystem for the period 1970–2004 by means of dynamic food web modelling. *Ecological Modelling* **274**, 41–49.

NOAA. 2020. Table of Cold & Warm ENSO Episodes by Season. Available at: https://origin.cpc.ncep.noaa.gov/ products/analysis_monitoring/ensostuff/ONI_v5.php (Accessed online 26.05.2020).

Ochoa, N., Taylor, M.H., Purca, S. & Ramos, E. 2010. Intra-and interannual variability of nearshore phytoplankton biovolume and community changes in the northern Humboldt Current system. *Journal of Plankton Research* **32**, 843–855.

Ohtsuka, S., Koike, K., Lindsay, D., Nishikawa, M.H., Kawahara, M., Mulyadi, N., Mujiono, N., Hiromi, J. & Komatsu, H. 2009. Symbionts of marine medusae and ctenophores. *Plankton and Benthos Research* **4**, 1–13.

Oliva, M.E., Maffet, A. & Laudien, J. 2010. Asociación entre *Chrysaora plocamia* (Cnidaria, Scyphozoa) e *Hyperia curticephala* (Peracarida: Amphipoda) en Bahía de Mejillones, norte de Chile. *Revista de biología marina y oceanografia* **45**, 127–130.

Oliveira, O.M.P., Araújo, E.M., Ayon, P., CedeñoPosso, C.M., Cepeda, A.A., Córdova, P., Cunha, A.F., Galea, H. Genzano, G.N., Haddad, M.A., Mianzan, H.W., Migotto, A.E., Miranda, L.S., Miranda, T.P., Morandini, A.C., Nagata, R.M., Nascimento, K.B., Nogueira Jr., M., Palma, S., Quiñones, J.A.D., Rodriguez, C.S., Scarabino, F., Schiariti, A., Stampar, S.N., Tronolone, V.B. & Marques, A.C. 2016. Census of Cnidaria (Medusozoa) and Ctenophora from South American marine waters. *Zootaxa* **4194**, 1–256.

Ommer, R.E., Jarre, A.C., Ian Perry, R., Barange, M., Cochrane, K. & Moloney, C. 2009. Human dimensions of the fisheries under global change. In *Climate Change and Small Pelagic Fish*, D.M. Checkley, J. Alheit, Y. Oozeki, & C. Roy et al. (eds). Cambridge: Cambridge University Press, pp. 275–284.

Opdal, A.F., Brodeur, R.D., Cieciel, K., Daskalov, G.M., Mihneva, V., Ruzicka, J.J., Verheye, H.M. & Aksnes, D.L. 2019. Unclear associations between small pelagic fish and jellyfish in several major marine ecosystems. *Scientific Reports* **9**, 2997, doi:10.1038/s41598-019-39351-7.

Pagès, F. 1992. Mesoscale coupling between planktonic cnidarian distribution and water masses during a temporal transition between active upwelling and abatement in the northern Benguela system. In Benguela Trophic Functioning, A.I.L. Payne, K.H. Brink, K.H. Mann & R. Hilborn (eds). *South African Journal of Marine Science* **12**, 41–52.

Pagès, F. & Gili, J-M. 1991a Vertical distribution of epipelagic siphonophores at the confluence between Benguela waters and the Angola Current over 48 hours. Hydrobiologia **216/217**, 355–362.

Pagès, F. & Gili, J-M. 1991b. Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Marine Ecology Progress Series* **75**, 205–215.

Pagès, F. & Gili, J-M. 1992 Influence of Agulhas waters on the population structure of planktonic cnidarians in the southern Benguela region. *Scientia Marina* **56**, 109–123.

Pagès, F., Gili, J-M. & Bouillon, J. 1992. Medusae (Hydrozoa, Scyphozoa, Cubozoa) of the Benguela Current (southeastern Atlantic). *Scientia Marina* **56**, 1–64.

Pagès, F. & Orejas, C. 1999. Medusae, siphonophores and ctenophores of the Magellan region. *Scientia Marina* **63**, 51–57.

Pagès, F., Verheye, H.M., Gili, J-M. & Flos, J. 1991. Short-term effects of coastal upwelling and wind reversals on assemblages of epiplanktonic cnidarians in the southern Benguela ecosystem. *South African Journal of Marine Science* **10**, 203–211.

Palma, S., Apablaza, P. & Silva, N. 2007. Hydromedusae (Cnidaria) of the Chilean southern channels (from Corcovado Gulf to Pulluche-Chacabuco Channels). *Scientia Marina* **71**, 65–74.

Palma, S., Córdova, P., Silva, N. & Silva, C. 2014. Biodiversity and spatial distribution of medusae in the Magellan Region (Southern Patagonian Zone). *Latin American Journal Aquatic Research* **42**, 1175–1188.

Palma, S., Silva, N., Retamal, M.C. & Castro, L. 2011. Seasonal and vertical distributional patterns of siphonophores and medusae in the Chiloé Interior Sea, Chile. *Continental Shelf Research* **31**, 260–271.

Palmieri, M.G., Barausse, A., Luisetti, T. & Turner, K. 2014. Jellyfish blooms in the Northern Adriatic Sea: Fishermen's perceptions and economic impacts on fisheries. *Fisheries Research* **155**, 51–58.

Palomares, M.L.D. & Pauly, D. 2009. The growth of jellyfishes. *Hydrobiologia* **616**, 11–21

Paredes, E. 2015. Hábitos alimentarios de la tortuga verde del Pacífico Este *Chelonia mydas agassizzi* (Boucort, 1868) en la bahía de Paracas, Ica, Perú, durante el año 2010. Universidad Nacional Mayor de San Marcos, Lima, Perú, 69 pp.

Parrish, R.H., Bakun, A., Husby, D.M. & Nelson, C.S. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. In: *Examine Changes in Abundance and Species Composition of Neritic Fish Resources*, G.D. Sharp & J. Csirke (eds). *Proceedings of the FAO Fisheries Report* **291**, 731–778.

Pauly, D. 1983. Length-converted catch curves. A powerful tool for fisheries research in the tropics. Part I. *Fishbyte* **1**, 9–13.

Pauly, D., Graham, W., Libralato, S., Morissette, L. & Palomares, M.D. 2009. Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia* **616**, 67–85.

Pearcy, W.G. 1972. Distribution and ecology of oceanic animals off Oregon. In *The Columbia River Estuary and Adjacent Ocean Waters*, A.T. Pruter & D.L. Alverson (eds). Seattle: University Washington Press, pp. 351–377.

Pearcy, W., Fisher, J., Brodeur, R. & Johnson, S. 1985. Effects of the 1983 El Niño on coastal nekton off Oregon and Washington. In *El Niño North: Niño Effects in the Subarctic Pacific Ocean*, W.S. Wooster & D.J. Fluharty (eds). Washington: Sea Grant Publications, pp. 188–204.

Pelegrí, J.L. & Benazzouz, A. 2015. Coastal upwelling off North-West Africa. In: *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem*, Valdés, L. & Déniz-González, I. (eds). Paris: IOC- UNESCO. *IOC Technical Series* **115**, 93–103.

Pelegrí, J.L, Marrero-Díaz, A., Ratsimandresy, A., Antoranz, A., Cisneros-Aguirre, J., Gordo, C., Grisolía, D., Hernández-GuerraI, A., Láiz, I., Martínez, A., Parrilla, G., Pérez-Rodríguez, P., Rodríguez-Santana, A. & Sangrà, P. 2005. Hydrographic cruises off northwest Africa: The Canary Current and the Cape Ghir region. *Journal of Marine Systems* **54** (1–4), 39–63.

Pelegrí, J.L. & Peña-Izquierdo, J. 2015. Eastern boundary currents off North-West Africa. In: *Oceanographic and biological features in the Canary Current Large Marine Ecosystem*, Valdés, L. & Déniz-González, I. (eds). Paris: IOC- UNESCO. *IOC Technical Series* **115**, 81–92.

Pennington, J.T., Mahoney, K.L., Kuwahara, V.S., Kolber, D.D., Calienes, R. & Chavez, F.P. 2006. Primary production in the eastern tropical Pacific: A review. *Progress in Oceanography* **69**, 285–317.

Perea, A. & Roque, C. 2005. Parámetros reproductivos de adultos de anchoveta peruana a finales del invierno 2005. *Informe Instituto del Mar del Perú* **35**, 167–171.

Peterson, W. 1998. Life cycle strategies of copepods in coastal upwelling zones. *Journal of Marine Systems* **15**, 313–326.

Peterson, W.T., Fisher, J.L., Strub, P.T., Du, X., Risien, C., Peterson, J. & Shaw, C.T. 2017. The pelagic ecosystem in the northern California Current off Oregon during the 2014–2016 warm anomalies within the context of the past 20 years. *Journal of Geophysical Research: Oceans* **122**, 7267–7290.

Pikitch, E.K., Rountos, K.J., Essington, T.E., Santora, C., Pauly, D., Watson, R., Sumaila, U.R., Boersma, P.D., Boyd, I.L. & Conover, D.O. 2014. The global contribution of forage fish to marine fisheries and ecosystems. *Fish and Fisheries* **15**, 43–64.

Pillar, S.C., Stuart, V., Barange, M. & Gibbons, M.J. 1992. Community structure and trophic ecology of euphausiids in the Benguela ecosystem. *South African Journal of Marine Science* **12**, 393–409.

Pitcher, G., Brown, P. & Mitchell-Innes, B. 1992. Spatio-temporal variability of phytoplankton in the southern Benguela upwelling system. *South African Journal of Marine Sci*ence **12**, 439–456.

Pitcher, G.C., Probyn, T.A., du Randt, A., Lucas, A.J., Bernard, S., Evers-King, H., Lamont, T. & Hutchings, L. 2014. Dynamics of oxygen depletion in the nearshore of a coastal embayment of the southern Benguela upwelling system. *Journal of Geophysical Research: Oceans* **119**, 2183–2200.

Pitt, K.A., Lucas, C.H., Condon, R.H., Duarte, C.M. & Stewart-Koster, B. 2018. Claims that anthropogenic stressors facilitate jellyfish blooms have been amplified beyond the available evidence: A systematic review. *Frontiers in Marine Science* **5**, 451, doi:10.3389/fmars.2018.00451.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **83**, 703–718.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G. & Montaña, J.C.G. 2007. Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**, 179–189.

Prieto, L., Armani, A. & Macías, D. 2013. Recent strandings of the giant jellyfish *Rhizostoma luteum* Quoy and Gaimard, 1827 (Cnidaria: Scyphozoa: Rhizostomeae) on the Atlantic and Mediterranean coasts. *Marine Biology* **160** (2): 3241–3247.

Prieto, L. Enrique-Navarro, A. Li Volsi, R. & Ortega, M.J. 2018. The large jellyfish *Rhizostoma luteum* as sustainable a resource for antioxidant properties, nutraceutical value and biomedical applications. *Marine Drugs* **16** (396), 1–10.

Prieto, L. & Idrissi, F.H. 2020. Jellyfish abundance on the shores in the Canary Current Large Ecosystem over 2009–2019 compiled by ICMAN (CSIC) and INRH. DIGITAL.CSIC, doi:10.20350/digitalCSIC/12681

Prieto, L., Macías, D., Peliz, A. & Ruiz, J. 2015. Portuguese Man-of-War (*Physalia physalis*) in the Mediterranean: A permanent invasion or a casual appearance? *Scientific Reports* **5**, 11545.

Purcell, J.E. 1989. Predation on fish larvae and eggs by the hydromedusa *Aequorea victoria* at a herring spawning ground in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **46**, 1415–1427.

Purcell, J.E. 1991. Predation by *Aequorea victoria* on other species of potentially competing pelagic hydrozoans. *Marine Ecology Progress Series* **72**, 255–260.

Purcell, J.E. 2009. Extension of methods for jellyfish and ctenophore trophic ecology to large-scale research. *Hydrobiologia* **616**, 23–50.

Purcell, J. E. 2010. Use of respiration rates of scyphozoan jellyfish to estimate their effects on the food web. *Hydrobiologia* **645**, 135–1520.

Purcell, J.E. & Arai, M.N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: A review. *Hydrobiologia* **451**, 27–44.

Purcell, J.E. & Grover, J.J. 1990. Predation and food limitation as causes of mortality in larval herring at a spawning ground in British Columbia. *Marine Ecology Progress* **59**, 55–61.

Purcell, J.E., Hoover, R.A. & Schwarck, N.T. 2009. Interannual variation of strobilation by the scyphozoan *Aurelia labiata* in relation to polyp density, temperature, salinity, and light conditions in situ. *Marine Ecology Progress Series* **37**, 139–149.

Purcell, J.E. & Sturdevant, M.V. 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Marine Ecology Progress* **210**, 67–83.

Purcell, J.E., Uye, S.I. & Lo, W.T. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: A review. *Marine Ecology Progress Series* **350**, 153–174.

Quiñones, J. 2008. *Chrysaora plocamia* Lesson, 1830 (Cnidaria, Scyphozoa), frente a Pisco, Perú. *Informe Instituto del Mar del Perú* **35**, 221–230.

Quiñones, J. 2018. Los Niños, Los Viejos, Las Medusas y su interacción con las pesquerías en el ecosistema norte de la Corriente de Humboldt, análisis de la medusa Scyphozoa Chrysaora plocamia. Tesis Doctorado, Universidad Nacional de Mar del Plata, Mar del Plata, 208 pp.

Quiñones, J., Carman, V.G., Zeballos, J., Purca, S. & Mianzan, H.W. 2010. Effects of El Niño-driven environmental variability on black turtle migration to Peruvian foraging grounds. *Hydrobiologia* **645**, 69–79.

Quiñones, J., Chiaverano, L.M., Ayón, P., Adams, G.D., Mianzan, H.W. & Acha, E.M. 2018. Spatial patterns of large jellyfish *Chrysaora plocamia* blooms in the Northern Humboldt Upwelling System in relation to biological drivers and climate. *ICES Journal of Marine Science* **75**, 1405–1415.

Quiñones, J., Mianzan, H.W., Purca, S., Robinson, K.L., Adams, G.D. & Acha, E.M. 2015. Climate-driven population size fluctuations of jellyfish (*Chrysaora plocamia*) off Peru. *Marine Biology* **162**, 2339–2350.

Quiñones, J., Monroy, A., Acha, E.M. & Mianzan, W.H. 2013. Jellyfish bycatch diminishes profit in an anchovy fishery off Peru. *Fisheries Research* **139**, 47–50.

Ralston, S., Sakuma, K.M. & Field, J.C. 2013. Interannual variation in pelagic juvenile rockfish abundance—going with the flow. *Fisheries and Oceanography* **22**, 288–308.

Rambaut, A., Drummond, A.J., Xie, D.G. & Suchard, M.A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67**, 901–904.

Rambaut, A. 2014. Figtree v1.4.2 (accessed April 2016). Available at http://tree.bio.ed.ac.uk/software/figtree/.

Ras, V., Neethling, S., Engelbrecht, A., Morandini, A.C., Bayha, K., Skrypzeck, H. & Gibbons M.J. 2020. There are three species of *Chrysaora* (Scyphozoa: Discomedusae) in the Benguela upwelling ecosystem, not two. *Zootaxa* **4778**, 401–438.

Raskoff, K.A. 2001. The impact of El Niño events on populations of mesopelagic hydromedusae. *Hydrobiologia* **451**, 121–129.

Raskoff, K.A. 2003. Collection and culture techniques for gelatinous zooplankton. *Biological Bulletin* **204**, 68–80.

Raskoff, K.A., Sommer, F.A., Hamner, W.A. & Cross, K.M. 2003. Collection and culture techniques for gelatinous zooplankton. *Biological Bulletin* **204**, 68–80.

Reum, J.C., Hunsicker, M.E. & Paulsen, C.E. 2009. Species composition and relative abundance of large medusae in Puget Sound, WA. *Northwest Science* **84**, 131–140.

Riascos, J.M., Carstensen, D., Laudien, J., Arntz, W.E., Oliva, M.E., Güntner, A. & Heilmayer, O. 2009. Thriving and declining: Climate variability shaping life-history and population persistence of *Mesodesma donacium* in the Humboldt Upwelling System. *Marine Ecology Progress Series* **385**, 151–163.

Riascos, J.M., Docmac, F., Reddin, C. & Harrod, C. 2015. Trophic relationships between the large scyphomedusa *Chrysaora plocamia* and the parasitic amphipod *Hyperia curticephala*. *Marine Biology* **162**, 1841–1848.

Riascos, J.M., Gutiérrez Aguilar, D.A., Escribano, R. & Thatje, S. 2019. El Niño-Southern Oscillation on a changing planet–consequences for coastal ecosystems. *Frontiers in Marine Science* **6**, 774.

Riascos, J.M., Paredes, L., González, K., Cáceres, I. & Pacheco, A.S. 2013a. The larval and benthic stages of the scyphozoan medusa *Chrysaora plocamia* under El Niño-La Niña thermal regimes. *Journal of Expermiental Marine Biology and Ecology* **446**, 95–101.

Riascos, J.M., Vergara, M., Fajardo, J., Villegas, V. & Pacheco, A.S. 2012. The role of hyperiid parasites as a trophic link between jellyfish and fishes. *Journal of Fisheries Biology* **81**, 1686–1695.

Riascos, J.M., Villegas, V., Cáceres, I., Gonzalez, J.E. & Pacheco, A.S. 2013b. Patterns of a novel association between the scyphomedusa *Chrysaora plocamia* and the parasitic anemone *Peachia chilensis*. *Journal of Marine Biology Association of the United Kingdom* **93**, 919–923.

Riascos, J.M., Villegas, V. & Pacheco, A.S. 2014. Diet composition of the large scyphozoan jellyfish *Chrysaora plocamia* in a highly productive upwelling centre off northern Chile. *Marine Biology Research* **10**, 791–798.

Rice, C.A., Duda, J.J., Greene, C.M. & Karr, J.R. 2012. Geographic patterns of fishes and jellyfish in Puget Sound surface waters. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* **4**: 117–128.

Richardson, A.J., Bakun, A., Hays, G.C. & Gibbons, M.J. 2009. The jellyfish joyride: Causes, consequences and management responses to a more gelatinous future. *Trends Ecology and Evoloution* **24**, 312–322.

Robinson, K.L., Ruzicka, J.J., Decker, M.B., Brodeur, R.D., Hernandez, F.J., Quiñones, J., Acha, J., Uye, S.-I., Mianzan, H.W. & Graham, W.N. 2014. Jellyfish, forage fish, and the world's major fisheries. *Oceanography* **27**, 104–115.

Roel, B.A. & Armstrong, M.J. 1991. The round herring *Etrumeus whiteheadi*, an abundant, underexploited clupeoid species off the coast of southern Africa. *South African Journal of Marine Science* **11**, 267–287.

Rogers, J. & Bremner, J.M. 1991. The Benguela Ecosystem. Part VII. Marine-geological aspects. *Oceanography and Marine Biology: Annual Review* **29**, 1–85.

Rottini Sandrini, L. & Avian, M. 1991. Reproduction of *Pelagia noctiluca* in the central and northern Adriatic Sea. *Hydrobiologia* **216**, 197–202.

Rouault, M. 2012. Bi-annual intrusion of tropical water in the northern Benguela upwelling. *Geophysical Research Letters* **39**, L12606.

Rouault, M., Illig, S., Bartholomae, C., Reason, C.J.C. & Bentamy, A. 2007. Propagation and origin of warm anomalies in the Angola Benguela upwelling system in 2001. *Journal of Marine Systems* **68**, 477–488.

Roux, J.-P. & Shannon, L.J. 2004. Ecosystem approach to fisheries management in the northern Benguela: The Namibian experience. In Ecosystem Approaches to Fisheries in the Southern Benguela, L.J. Shannon, K.L. Cochrane & S.C. Pillar (eds). *African Journal of Marine Science* **26**, 79–93.

Roux, J.-P., van der Lingen, C.D., Gibbons, M.J., Moroff, N.E., Shannon, L.J., Smith, A.D.M. & Cury, P.M. 2013. Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fish: Lessons from the Benguela. *Bulletin of Marine Science* **89**, 249–284.

Roy, C. 1991. Les upwellings: le cadre physique des pêcheries côtières ouest-africaines. In *Pêcheries Ouest–africaines. Variabilité, Instabilité et Changement*, P. Cury & C. Roy (éds.). Paris: ORSTOM, pp. 38–66.

Russell, F. 1970. *The Medusae of the British Isles II. Pelagic Scyphozoa with a Supplement to the First Volume on Hydromedusae*. Cambridge: Cambridge University Press.

Rutllant, J.A., Rosenbluth, B. & Hormazábal, S. 2004. Intraseasonal variability of wind-forced coastal upwelling off central Chile (30°S). *Continental Shelf Research* **24**, 789–804.

Ruzicka, J.J., Brodeur, R.D., Emmett, R.L., Steele, J.H., Zamon, J.E., Morgan, C.A., Thomas, A.C. & Wainwright, T.C. 2012. Interannual variability in the Northern California current food web structure: Changes in energy flow pathways and the role of forage fish, euphausiids, and jellyfish. *Progress in Oceanography* **102**, 19–41.

Ruzicka, J.J., Brodeur, R.D. & Wainwright, T.C. 2007. Seasonal food web models for the Oregon inner-shelf ecosystem: Investigating the role of large jellyfish. *California Cooperative Oceanic Fisheries Investigations Reports* **48**, 106–128.

Ruzicka, J.J., Daly, E.A. & Brodeur, R.D. 2016. Evidence that summer jellyfish blooms impact Pacific Northwest salmon production. *Ecosphere* **7**, e01324, doi:10.1002/ecs2.1324

Ruzicka, J., Brodeur, R., Cieciel, K. & Decker, M.B. 2020. Examining the ecological role of jellyfish in the Eastern Bering Sea ecosystem. *ICES Journal of Marine Science* **2**, 791–802.

Ruzicka, J.J., Steele, J.H., Gaichas, S.K., Ballerini, T., Gifford, D.J., Brodeur, R.D. & Hofmann, E.E. 2013. Analysis of energy flow in US GLOBEC ecosystem using end-to-end models. *Oceanography* **26**, 82–97.

Rykaczewski, R.R. & Checkley, D.M. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proceedings of the National Academy of Sciences* **105**, 1965–1970.

Ryther, J.H. 1969. Photosynthesis and Fish Production in the Sea. *Science* **166**, 72–76.

Sakuma, K.M., Field, J.C., Marinovic, B.B., Carrion, C.N., Mantua N.J. & Ralston. S. 2016. Anomalous epipelagic micronekton assemblage patterns in the neritic waters of the California Current in spring 2015 during a period of extreme ocean conditions. *California Cooperative Oceanic Fisheries Investigations Reports* **57**, 163–183.

Salvanes, A.G.V., Bartholomae, C., Yemane, D., Gibbons, M.J., Kainge, P., Krakstad, J-O., Rouault, M., Staby, A. & Sundby, S. 2015. Spatial dynamics of the bearded goby and its key fish predators off Namibia varies with climate and oxygen availability. *Fisheries Oceanography* **24**(Suppl. 1), 88–101.

Salvatteci, R., Field, D., Gutiérrez, D., Baumgartner, T., Ferreira, V., Ortlieb, L., Sifeddine, A., Grados, D. & Bertrand, D. 2018. Multifarious anchovy and sardine regimes in the Humboldt Current System during the last 150 years. *Global Change Biology* **24**, 1055–1068.

Samhouri, J.F., Levin, P.S. & Ainsworth, C.H. 2010. Identifying thresholds for Ecosystem-Based Management. *PLoS One* **5**, e8907, doi:10.1371/ journal.pone.0008907

Santora, J.A., Field, J.C., Schroeder, I.D., Sakuma, K.M., Wells, B.K. & Sydeman, W.J. 2012. Spatial ecology of krill, micronekton and top predators in the central California Current: Implications for defining ecologically important areas. *Progress in Oceanography* **106**, 154–174.

Schiariti, A., Christiansen, E., Morandini, A.C., Da Silveira, F.L., Giberto, D.A. & Mianzan, H.W. 2012. Reproductive biology of Lychnorhiza lucerna (Cnidaria: Scyphozoa: Rhizostomeae): Individual traits related to sexual reproduction. *Marine Ecology Research* **8**, 255–264.

Schiariti, A., Dutto, M.S., Pereyra, D.Y., Siquier, G.F. & Morandini, A.C. 2018. Medusae (Scyphozoa and Cubozoa) from southwestern Atlantic and Subantarctic region (32–60°S, 34–70°W): Species composition, spatial distribution and life history traits. *Latin American Journal of Aquatic Research* **46**, 240–257.

Schuchert, P. 2020. *Aequorea forskalea* Péron & Lesueur, 1810. World Register of Marine Species: http://www.marinespecies.org/ aphia.php?p=taxdetails&id=117270 (accessed on 2020-8-7).

Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, E.E., Maccall, A.D., Matsuura, Y., Nevárez-Martínez, M.O., Parrish, R.H., Roy, C., Serra, R., Shust, K.V., Ward, M.N. & Zuzunaga, J.Z. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science* **21**, 289–347.

Schweigger, E. 1964. *El litoral peruano*. Lima: Universidad Nacional Federico Villareal, 435 pp.

Serrano, A.L. 2016. *Settling patterns of Chrysaora quinquecirrha polyps on common vinyl construction material: Potential implications for jellyfish blooms and coastal development in Barnegat Bay New Jersey*. Unpublished Master's thesis, Montclair State University, 57 pp.

Shackleton, L.Y. 1987. A comparative study of fossil fish scales from three upwelling regions. *South African Journal Marine Science* **5**, 79–84.

Shaffer, G., Hormázabal, S., Pizarro, O. & Salinas S. 1999. Seasonal and interannual variability of currents and temperature off central Chile. *Journal of Geophysical Research - Oceans* **104**, 29951–29961.

Shannon, L., Coll, M., Neira, S., Cury, P. & Roux, J.-P. 2009. Impacts of fishing and climate change explored using trophic models. In *Climate Change and Small Pelagic Fish*, D. Checkley, C. Roy, J. Alheit & Y. Oozebi et al. (eds). Cambridge: Cambridge University Press, pp. 158–190.

Shannon, L.J., Cury, P.M. & Jarre, A. 2000. Modelling effects of fishing in the Southern Benguela ecosystem. *ICES Journal of Marine Science* **57**, 720–722.

Shannon, L.J. & Jarre-Teichmann, A. 1999. A model of trophic flows in the northern Benguela upwelling ecosystem during the 1980s. *South African Journal of marine Science* **21**, 349–366.

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

Shannon, L.V. & Chapman, P. 1983. Incidence of *Physalia* on Beaches in the South Western Cape Province during January 1983. *South African Journal of Science* **79**, 454–458.

Shannon, L.V., Hempel, G., Malanotte-Rizzoli, P., Moloney, C.L. & Woods, J. (eds). 2006. *Benguela: Predicting a Large Marine Ecosystem*. Large Marine Ecosystems 14. Amsterdam: Elsevier, 410pp + CD-ROM.

Shannon, L.V. & Pillar, S.C. 1986. The Benguela ecosystem, part 3. Plankton. *Oceanography and Marine Biology: An Annual Review* **24**, 65–170.

Shelton, P.A. 1992. Detecting and incorporating multi-species effects into fisheries management in the north-west and south-east Atlantic. *South African Journal Marine Science* **12**, 723–735.

Shenker, J.M. 1985. Carbon content of the neritic scyphomedusa *Chrysaora fuscescens*. *Journal of Plankton Research* **7**,169–173.

Sheppard, C. (ed.) 2019. *World Seas: An Environmental Evaluation*. Volume I: Europe, the Americas and West Africa. London: Academic Press.

Sherman, K. & Alexander, L.M. (eds). 1986. Variability and management of Large Marine Ecosystems. *American Association for the Advancement of Science (AAAS) Selected Symposium 99*. Boulder, ColoradoCO: Westview Press, 319.

Shoji, J., Masuda, R., Yamashita, Y. & Tanaka, M. 2005. Effect of low dissolved oxygen concentrations on behavior and predation rates on red sea bream *Pagrus major* larvae by the jellyfish *Aurelia aurita* and by juvenile Spanish mackerel *Scomberomorus niphonius*. *Marine Biology* **147**, 863–868.

Shushkina, E.A., Musaeva, E.I., Anokhina, L.L. & Lukasheva, T.A. 2000. Role of the gelatinous macroplankton: jellyfish *Aurelia* and invading ctenophores *Mnemiopsis* and *Beroe* in the plankton communities of the Black Sea. *Oceanologya* **40**, 859–866 (in Russian).

Sibeene, P. 2006. Namibia: Seals starving to death. *New era*. https://allafrica.com/stories/200612181417.html (accessed September 25, 2019).

Silva, G., Horne, J.B. & Castilho, R. 2014. Anchovies go north and west without losing diversity: Post-glacial range expansions in a small pelagic fish. *Journal of Biogeography* **41**, 1171–1182.

Simmonds, J. & MacLennan, D.N. 2005. *Fisheries Acoustics: Theory and Practice*. Blackwell: John Wiley & Sons.

Skrypzeck, H. 2019. Observations on the ecology and life-history of *Chrysaora fulgida* (Reynaud 1830) (Scyphozoa: Semaeostomeae) and other pelagic cnidarians in the inshore waters off central Namibia. PhD thesis. University of Western Cape, Cape Town, 105 pp.

Skrypzeck, H. & Gibbons, M.J. (2021). The persistent presence of *Chrysaora fulgida* (Scyphozoa; Discomedusae) in the northern Benguela ecosystem is not reflected by constant recruitment. *Journal of Plankton Research* **43**, 72–84.

Skrypzeck, H., van der Lingen, C.D. & Gibbons, M.J. (2021). Cross shelf movement of *Chrysaora fulgida* (Scyphozoa; Discomedusae) off Namibia inferred from stable isotopes (δ15N and δ13C). *South African Journal of Marine Science* **43**, 87–93.

Smit, J. & Hertogen, J. 1980. An extraterrestrial event at the Cretaceous-Tertiary boundary. *Nature* **285**, 198–200.

Smith, A.D.M., Brown, C.J., Bulman, C.M., Fulton, E.A., Johnson, P., Kaplan, I.C., Lozano-Montes, H., Mackinson, S., Marzloff, M., Shannon, L.J., Shin, Y-J. & Tam, J. 2011. Impacts of fishing low trophic level species on marine ecosystems. *Science* **333**, 1147–1150.

Snyder, M.A., Sloan, L.C., Diffenbaugh, N.S. & Bell, J.L. 2003. Future climate change and upwelling in the California Current. *Geophysical Research Letters* **30**, 1823, doi:10.1029/2003GL017647

Somers, I.F. 1988. On a seasonally oscillating growth function. *Fishbyte* **6**, 8–11.

Sorenson, H.L. 2018. *Population dynamics and variability of two gelatinous zooplankters (*Aequorea *and* Pyrosoma atlanticum*) in the Northern California Current*. Master's thesis, University of Oregon, Eugene, Oregon, USA, 44 pp.

Sparks, C., Brierley, A.S., Buecher, E., Boyer, D., Axelsen, B.E. & Gibbons, M.J. 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 UK* **85**, 519–522.

Sparks, C., Buecher, E., Brierley, A.S., Boyer, H., Axelsen, B.E. & Gibbons, M.J. 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, G.H. & De Decker, A.H.B. 1969. Some physical and biological aspects of an oceanographic anomaly off South West Africa in 1963. Investigational Report, Marine Research Laboratory, no. 81. Walvis Bay, Namibia: Marine Research Laboratory.

Steele, J.H. & Ruzicka, J.J. 2011. Constructing end-to-end models using ECOPATH data. *Journal of Marine Systems* **87**, 227–238.

Steger, J.M., Schwing, F.B., Collins, C.A., Rosenfeld, L.K., Garfield, N. & Gezgin, E. 2000. The circulation and water masses in the Gulf of the Farallones. *Deep-Sea Research II* **47**, 907–946.

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

Straehler-Pohl, I. 2020. Ernst Haeckel's mysterious species, Part I: The validity of *Carybdea murrayana* Haeckel, 1880 (Cubomedusae) and revisional notes on Haeckel's other Carybdeidae. *Plankton and Benthos Research* **15**, 1–29.

Strømme, T., Lipinski, M.R. & Kainge, P. 2016. Life cycle of hake and likely management implications. *Reviews in Fish Biology and Fisheries* **26**, 235–248.

Strub, P.T., Kosro, P.M. & Huyer, A. 1991. The nature of the cold filaments in the California Current System. *Journal of Geophysical Research* **96**, 14743–14768.

Suchman, C.L. & Brodeur, R.D. 2005. Abundance and distribution of large medusae in surface waters of an upwelling zone off coastal Oregon, USA. *Deep Sea Research II* **52**, 51–72.

Suchman, C.L., Brodeur, R.D., Emmett, R.L. & Daly, E.A. 2012. Large medusae in surface waters of the Northern California Current: Variability in relation to environmental conditions. *Hydrobiologia* **690**, 113–125.

Suchman, C.L., Daly, E.A., Keister, J.E., Peterson, W.T. & Brodeur, R.D. 2008. Feeding patterns and predation potential of scyphomedusae in a highly productive upwelling region. *Marine Ecological Progress Series* **358**, 161–72.

Swift, H.F. & Dawson, M.N. 2020. Demographic, environmental, and phenotypic change but genetic consistency in the jellyfish *Mastigias papua*. *Biological Bulletin* **239**,

Sydeman, W.J., García-Reyes, M., Schoeman, D., Rykaczewski, R.R., Thompson, S.A., Black, B.A. & Bograd, S.J. 2014. Climate change and wind intensification in coastal upwelling ecosystems. *Science* **345**, 77–80, doi:10.1126/science.1251635

Takahashi, K. 2005. The annual cycle of heat content in the Peru Current region. *Journal of Climate* **18**, 4937–4954.

Tam, J., Taylor, M.H., Blaskovic V., Espinoza, P., Ballón, R.M., Díaz, E., Ballón, M., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quipuzcoa, L., Gutiérrez, D., Goya, E., Ochoa, N., & Wolff, M.I. 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part I: Comparing trophic linkages under La Niña and El Niño conditions. *Progress in Oceanography* **79**, 352–365.

Taylor, M.H., Tam J., Blaskovic V., Espinoza P., Ballón R.M., Wosnitza-Mendo C., Ballón, M., Díaz, E., Wosnitza-Mendo, C., Argüelles, J., Purca, S., Ayón, P., Quipuzcoa, L., Gutiérrez, D., Goya, E., Ochoa, N., & Wolff, M.I. 2008. Trophic modeling of the Northern Humboldt Current Ecosystem, Part II: Elucidating ecosystem dynamics from 1995 to 2004 with a focus on the impact of ENSO. *Progress in Oceanography* **79**, 366–378.

Teves, N & Evangelista, E. 1974. Las 200 millas de mar territorial peruano y sus fondos marinos. *Boletín de la Sociedad Geológica del Perú* **53**, 59–74.

Thiel, M., Macaya, E.C., Acuña, E., Bastias, H., Brokordt, K., Camus, P.A., Castilla, J.C., Castro, L.R., Cortés, M., Dumont, C.P., Escribano, R., Fernández, M., Gajardo, J.A., Gaymer, C.F., Gomez, I., González, A.E., González, H.E., Haye, P.A., Illanes, J.-E., Iriarte, J.L., Lancellotti, D.A., Luna-Jorquera, G., Luxoro, C., Manríquez, P.H., Marín, V., Muñoz, P., Navarrete, S.A., Perez, E., Poulin, E., Sellanes, J., Sepúlveda, H.H., Stotz, W., Tala, F., Thomas, A., Vargas, C.A., Vasquez, J.A. & Alonso Vega, J.M. 2007. The Humboldt Current System of northern and central Chile-Oceanographic processes, ecological interactions and socioeconomic feedback. *Oceanography and Marine Biology: An Annual Review* **45**, 195–344.

Thiriot, A. 1978. Zooplankton communities in the West African upwelling area. In: *Analysis of Upwelling Systems*. R. Boje & M. Tomczak (eds). Berlin: Springer, pp. 32–60.

Tilves, U., Purcell, J.E., Fuentes, V.L., Torrents, A., Pascual, M., Raya, V., Gili, J.-M. & Sabatés, A. 2016. Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean. *Journal of Plankton Research* **38**, 1243–1254.

Tourre, Y.M., Lluch-Cota, S.E. & White, W.B. 2007. Global multi-decadal ocean climate and small-pelagic fish population. *Environmental Research Letters* **2**, 034005, 9 pp.

Towanda, T. & Theusen, E.V. 2006. Ectosymbiotic behavior of *Cancer gracilis* and its trophic relationships with its host *Phacellophora camtschatica* and the parasitoid *Hyperia medusarum*. *Marine Ecology Progress Series* **315**, 221–236.

Tredick, C.A., Lewison, R.L., Deutschman, D.H., Hunt, T.A., Gordon, K.L. & von Hendy, P. 2017. A rubric to evaluate citizen-science programs for long-term ecological monitoring. *BioScience* **67**, 834–844.

Treible, L.M. & Condon, R.H. 2019. Temperature-driven asexual reproduction and strobilation in three Scyphozoan jellyfish polyps. *Journal of Experimental Marine Biology and Ecology* **520**, 151204.

Unterüberbacher, H.K. 1964. The Pilchard of South West Africa (*Sardinops ocellata*): Zooplankton studies in the waters off Walvis Bay with special reference to the Copepoda. *Investigative Reports of Marine Research Lab. S.W. Africa* **11**, 2–36.

Utne-Palm, A.C., Salvanes, A.G.V., Currie, B., Kaartvedt, S., Nilsson, G.E., Braithwaite, V.A., Stecyk, J.A.W., Hundt, M., van der Bank, M., Flynn, B., Sandvik, G.K., Klevjer, T.A., Sweetman, A.K., Brüchert, V., Pittman, K., Peard, K.R., Lunde, I.G., Strandabø, R.A.U. & Gibbons, M.J. 2010. Trophic structure and community stability in an overfished ecosystem. *Science* **329**, 333–336

Valdés, L. & Dénis-Gónzález, I. (eds). 2015. *Oceanographic and Biological Feautures in the Canary Current Large Marine Ecosystem*. Paris: IOC-UNESCO. *IOC Technical Series* **115**, 383 pp.

van der Bank, M.G., Utne-Palm, A.C., Pittman, K., Sweetman, A.K., Richoux, N.B., Brüchert, V. and Gibbons, M.J. 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, C.D., Hutchings, L. & Field, J.G. 2006. Comparative trophodynamics of anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the southern Benguela: Are species alternations between small pelagic fish trophodynamically mediated? *African Journal of Marine Science* **28**, 465–477.

van der Lingen, C.D. 1994. Effect of particle size and concentration on the feeding behaviour of adult pilchard *Sardinops sagax*. *Marine Ecological Progress Series* **109**, 1–13.

van der Lingen, C.D., Bertrand, A., Bode, A., Brodeur, R., Cubillos, L., Espinoza, P., Friedland, K., Garrido, S., Irigoien, X., Miller, T., Möllman, C., Rodriguez-Sanchez, R., Tanaka, H. & Temming, A. 2009. Trophic dynamics. In *Climate Change and Small Pelagic Fish*, D.M. Checkley, C. Roy, J. Alheit, & Y. Oozeki et al. (eds). Cambridge, UK: Cambridge University Press, pp. 112–157.

Vélez-Belchí, P., González-Carballo, M., Pérez-Hernández, M.D. & Hernández-Guerra, A. 2015. Open ocean temperature and salinity trends in the Canary Current Large Marine Ecosystem. In: *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem*, L. Valdés & I. Déniz-González (eds). Paris: IOC-UNESCO. *IOC Technical Series* **115**, pp. 299–308. URI: http://hdl.handle.net/1834/9196.

Venter, G.E. 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, H.M., Hutchings, L., Huggett, J.A. & Painting, S.J. 1992. Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. *South African Journal of Marine Science* **12**, 561–584.

Verheye, H.M., Lamont, T., Huggett, J.A., Kreiner, A. & Hampton, I. 2016. Plankton productivity of the Benguela Current Large Marine Ecosystem (BCLME). *Environmental Development* **17**, 75–92.

Verheye, H.M., Richardson, A.J., Hutchings, L., Marska, G. & Gianakouros, D. 1998. Long-term trends in the abundance and community structure of coastal zooplankton in the southern Benguela system, 1951–1996. *South African Journal of Marine Science* **19**, 317–332.

Viñas, M.D., Blanco-Bercial, L., Bucklin, A., Verheye, H., Bersano, J.G.F. & Ceballos, S. 2015. Phylogeography of the copepod *Calanoides carinatus* s.l. (Krøyer) reveals cryptic species and delimits *C. carinatus s.s.* distribution in SW Atlantic Ocean. *Journal of Experimental Marine Biology Ecology* **468**, 97–104.

Walsh, J.J. 1981. A carbon budget for overfishing off Peru. *Nature* **290**, 300–304.

Walter, C., Christensen, V. & Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* **7**, 139–172.

Wang, B., Luo, X., Yang, Y.M., Sun, W., Cane, M.A., Cai, W., Yeh, S-W & Liu, J. 2019. Historical change of El Niño properties sheds light on future changes of extreme El Niño. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 22512–22517.

Wang, D., Ouhier, T.C., Menge, B.A. & Ganguly, A.R. 2015. Intensification and spatial homogenization of coastal upwelling under climate change. *Nature* **518**, 390–394.

Wang, P., Zhang, F., Liu, M.-T., Sun, S. & Xian, H. 2020. Isotopic evidence for size-based dietary shifts in the jellyfish *Cyanea nozakii* in the northern East China Sea. *Journal of Plankton Research*

Ware, D.M. & Thomson, R.E. 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *Science* **308**, 1280–1284.

Watermeyer, K.E., Hutchings, L., Jarre, A. & Shannon, L.J. 2016. Patterns of Distribution and Spatial Indicators of Ecosystem Change Based on Key Species in the Southern Benguela. *PLoS ONE* **11**(7), e0158734.

Watermeyer, K.E., Shannon, L.J., Roux, J.-P. & Griffiths, C.L. 2008. Changes in the trophic structure of the northern Benguela before and after the onset of industrial fishing. *African Journal of Marine Science* **30**, 383–403.

Wetherall, A. 1986. A new method for estimating growth and mortality parameters from length frequency data. *Fishbyte* (ICLARM/The WorldFish Center) **4**(1), 12–14.

Widmer, C.L. 2005. Effects of temperature on growth of north-east Pacific moon jellyfish ephyrae, *Aurelia labiata* (Cnidaria: Scyphozoa). *Journal of the Marine Biological Association of the United Kingdom* **85**, 569–574.

Widmer, C.L. 2006. Life cycle of *Phacellophora camtschatica* (Cnidaria: Scyphozoa). *Invertebrate Biology* **125**, 83–90.

Widmer, C.L. 2008a. *How to Keep Jellyfish in Aquariums: An Introductory Guide for Maintaining Healthy Jellies*. Tucson, USA: Wheatmark.

Widmer, C.L. 2008b. Life cycle of *Chrysaora fuscescens* (Cnidaria: Scyphozoa) and a key to sympatric ephyrae 1. *Pacific Science* **62**, 71–82.

Wooster, W.S., Bakun A. & McLain D.R. 1976. The seasonal upwelling cycle along the eastern boundary of the north Atlantic. *Journal of Marine Research* **34**, 131–141.

Wright, R.M., le Quéré, C., Buitenhuis, E., Pitois, S. & Gibbons, M.J. 2020. Unique role of jellyfish in the plankton ecosystem revealed using a global ocean biogeochemical model. *Biogeosciences* **136**, 1–43.

Wrobel, D. & Mills, C. 1998. *Pacific Coast Pelagic Invertebrates*. Monterey, CaliforniaCA: Monterey Bay Aquarium.

Zeman, S.M. 2015. *Orientation behavior and feeding ecology of the Scyphomedusa Chrysaora fuscescens*. Master's Thesis, University of Oregon, Eugene, Oregon, USA, 57 p.

Zeman, S.M., Brodeur, R.D., Daly, E.A & Sutherland, K.R. 2016. Prey selection patterns of *Chrysaora fuscescens* in the northern California Current. *Journal of Plankton Research* **38**, 1433–1443.

Ziegler, L. & Gibbons M.J. 2018. Environmental responses of jellyfish polyps as drivers of medusa populations off the coast of Namibia. *African Journal of Marine Science* **40**, 323–329.

Zwolinski, J.P., Demer, D.A., Byers, K.A, Cutter, G.R., Renfree, J.S., Sessions, T.S. & Macewicz, B. J. 2012. Distributions and abundances of Pacific sardine (*Sardinops sagax*) and other pelagic fishes in the California Current Ecosystem during spring 2006, 2008, and 2010, estimated from acoustic-trawl surveys. *Fishery Bulletin* **110**, 110–122.

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