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To cite this article: S. Rossi, C. Gravili, G. Milisenda, M. Bosch-Belmar, D. De Vito & S. Piraino (2019) Effects of global warming on reproduction and potential dispersal of Mediterranean Cnidarians, The European Zoological Journal, 86:1, 255-271, DOI: [10.1080/24750263.2019.1631893](https://doi.org/10.1080/24750263.2019.1631893)

To link to this article: <https://doi.org/10.1080/24750263.2019.1631893>



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Published online: 22 Jul 2019.



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REVIEW

Effects of global warming on reproduction and potential dispersal of Mediterranean Cnidarians

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(Received 28 September 2018; accepted 22 May 2019)

Abstract

Water temperature directly affects life cycles, reproductive periods, and metabolism of organisms living the oceans, especially in the surface zones. Due to the ocean warming, changes in water stratification and primary productivity are affecting trophic chains in sensitive world areas, such as the Mediterranean Sea. Benthic and pelagic cnidarians exhibit complex responses to climatic conditions. For example, the structure and phenology of the Mediterranean hydrozoan community displayed marked changes in species composition, bathymetric distribution, and reproductive timing over the last decades. The regional species pool remained stable in terms of species numbers but not in terms of species identity. When the Scyphozoa group is considered, we observe that *Pelagia noctiluca* (among the most abundant jellyfish in the Mediterranean Sea and eastern Atlantic waters) has increasingly frequent massive outbreaks associated to warmer winters. Variations in metabolic activities, such as respiration and excretion, are strongly temperature-dependent, with direct increment of energetic costs with jellyfish size and temperature, leading to growth rate reduction. Water temperature affects sexual reproduction through changes in the energy storage and gonad development cycles. Anthozoan life cycles depend also on primary productivity and temperature: gonadal production and spawning are tightly related in shallow populations (0–30 m depth) with the spring-summer temperature trends and autumn food availability. Overall, the energy transferred from the mother colonies to the offspring may decrease, negatively affecting their potential to settle, metamorphose and feed during the first months of their lives, eventually impairing the dominance of long-living cnidarian suspension feeders in shallow benthic habitats. In this review, we describe the already ongoing effects of sea warming on several features of cnidarian reproduction, trying to elucidate how reproductive traits and potential dispersion will be affected by the cascade effects of increasing temperature in the Mediterranean Sea.

Keywords: Climate change, reproduction, trophic ecology, larva, Cnidaria

Introduction

Fast temperature increase in the Mediterranean Sea waters has been crucial to understand pelagic and benthic community changes (Garrabou et al. 2009; Crisci et al. 2011). Despite slower, the velocity of climate change and seasonal shift in the oceans are as high as on land and often deviate from simple expectations of poleward migration and earlier

springs/late falls (Burrows et al. 2011). These community shifts, now evident all around the World, are even faster in this warm temperate sea (Shaltout & Omstedt 2014). The phenomena related to warming will increase faster in this area of the world because of the limited water masses and the related circulation that is previewed to change during the next decades (Galli et al. 2017). In fact, temperature

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raise in surface waters has been around $0.24^{\circ}\text{C decade}^{-1}$ in the west of the Strait of Gibraltar and $0.51^{\circ}\text{C decade}^{-1}$ over the Black Sea (Shaltout & Omstedt 2014), being also the deep waters affected by the warming phenomenon ($0.1\text{--}0.27^{\circ}\text{C decade}^{-1}$, García-Martínez et al. 2017).

The Mediterranean basin has a high rate of species endemism (28% of species are endemic), which may be predisposed to local extinction in such a fast-changing environment (Boero & Gravili 2013; Gravili et al. 2015a; Galli et al. 2017; García-Martínez et al. 2017). Several studies started focusing on the community and species repercussions of such warming tendency in this semi-closed area (Calvo et al. 2011; Goffredo & Dubinsky 2014). For example, studies of Lejeune et al. (2010), focused on the effects of climate change on the Mediterranean biota, concluded that warming of water masses affects the marine ecosystems, being complex to distinguish the effects of the local anthropic activities from those due to natural events. Almost two decades ago, it was already highlighted that the spread of alien species and its fast distribution northwards and from the east to the west may be due to the fact that some temperature physical barriers are weaker (Bianchi & Morri 2000). Actually, the progressive warming of the Mediterranean shallow waters is influencing the delicate coexistence of boreal, temperate, sub-tropical and tropical species (Moschella 2008; Corriero et al. 2015; Longobardi et al. 2017). Many of these deep environmental changes and its repercussions on single species or whole ecosystem functioning have been highlighted, such as the more frequent occurrence of harmful algal blooms (Mangialajo et al. 2010; Faimali et al. 2012; Privitera et al. 2012), mass mortalities of sponges and anthozoans in shallow waters (Cerrano et al. 2000; Linares et al. 2005; Garrabou et al. 2009; Rivetti et al. 2014; Parravicini et al. 2015), and changes in biodiversity of Mediterranean communities (Puce et al. 2009; Gatti et al. 2015; Gravili et al. 2015a; Betti et al. 2017a, and references therein).

One of the mechanisms of species adaptation to global warming is phenology (the synchronous timing of ecological events) and shifting biogeographic ranges (Parmesan & Yohe 2003; Thackeray et al. 2010; Burrows et al. 2011). Species phenology, mainly regulated by temperature and photoperiod (Hughes 2000; Boero et al. 2016), can provide a sensitive indicator of climate change (Visser et al. 1998; Bergmann 1999; Crick & Sparks 1999; Edwards & Richardson 2004, and references therein). Distribution and phenology are directly related with the physiology of the affected organisms, which, in turn, is directly influenced by the

temperature increase (Hughes 2000). The susceptibility to global climate change varies according to their biology and, inevitably, alters the interactions between species and their competitiveness (Hughes 2000; Harley et al. 2006; Moschella 2008). Yet, the available information in the Mediterranean area is still scarce and the future scenarios are still not clear (Boero et al. 2008b).

In fact, the level of response to climate change, associated with changes in phenology, may vary across the community and the seasonal cycle of the different species, leading to acclimation responses (i.e. accommodating their cycles of activity to the new environmental conditions) (Boero et al. 2008a). Temperature influences the metabolic rates of all organisms affecting numerous processes at the level of individuals, populations, and communities (O'Connor et al. 2007). In-depth study of the species response is needed to make a complete map of future distributions, local extinctions and new relationships among organisms. It is now clear that a modest increase in sea surface temperature may have significant effects on individuals with increasing rates of colony and population growth (Lough & Barnes 2000; Edmunds et al. 2005), and larval development (O'Connor et al. 2007). Such metabolic shifts are now happening, and its repercussions will structure the future ecosystem functioning.

Among these repercussions, reproduction is one of the most highlighted when trying to understand shifts in life-cycle trends and potential dispersion of the species. Reproduction may be considered one of the keys to understand the distribution and resistance of species in front of such physical changes. Successful or non-successful reproductive traits will be one of the most important factors explaining species presence and geographical shifts (Goffredo & Dubinsky 2016). Reproduction is related not only with temperature but also with the available autotrophic or heterotrophic inputs (Rossi et al. 2017). Changes in primary productivity and water stratification, due to the water warming, are thus affecting trophic chains in sensitive world areas, such as the Mediterranean Sea (Milisenda et al. 2017), inducing a mismatch between functional groups and trophic levels (Edwards & Richardson 2004). The Mediterranean, therefore, is an ideal framework, because of the accelerating path is present both in temperature but also in productivity, helping to visualize what could happen in future scenarios (Goffredo & Dubinsky 2014).

Understanding the reproductive traits under a climate change framework will thus help in the complex puzzle of future distribution and

survivorship of species (Lartaud et al. 2017). One of the most important taxonomic groups in terms of biomass, biodiversity and ecosystem functioning in the oceans are cnidarians (Goffredo & Dubinsky 2016). Benthic and pelagic cnidarians may be a very good example to understand the effects of sea warming and changes in productivity of water masses. These organisms exhibit composite responses to climatic conditions. Practically ubiquitous in all aquatic habitats, they are characterized by high regenerative capacity and considerable ability to form symbioses with microorganisms (Bosch et al. 2014; Sun et al. 2016; Schubert et al. 2017). They are morphologically simple but with complex gene repertoires able to code much of the sensory capacity of more complex animals (Technau et al. 2005; Chapman et al. 2010; Srivastava et al. 2010; Bosch et al. 2014). Many cnidarian species reproduce asexually by budding or colony fragmentation, and early embryos enable clonal propagation capacity due to recovery after fragmentation (Heyward & Negri 2012).

In cnidarian phenology and reproduction, temperature plays a critical role mediating life-cycle transitions (Bosch et al. 2014): generally, their larvae are motile but most adult stages (except in medusa) are sessile and, therefore, constantly exposed to changing environments. Reproduction may be thus positively or negatively affected by temperature, reducing or increasing fecundity, egg quality, fertilization success, and larval survivorship in this taxonomic group (Baird et al. 2009; Lartaud et al. 2017; Rossi et al. 2017; see McClanahan et al. 2009 for a review).

The present work considers a series of case studies in reproductive traits across three cnidarian classes: Hydrozoa, Scyphozoa, Anthozoa. We focus on the consequences of the last decades of Mediterranean warming and review the responses in the phenology and physiology of organisms with particular regard to some aspects of their reproductive processes that can be considered critical for their future in terms of distribution and adaptation to the new conditions.

Hydrozoa

Together with calcispongiae and colonial ascidians, hydroids are the most important suspension feeders group subjected to evident seasonal variations (Gaino et al. 1996; Gili et al. 1998; Bavestrello et al. 2006; Rossi et al. 2012). Species belonging to the Hydrozoa inhabit all aquatic ecosystems and display a wide array of life-cycle strategies (lateral

budding, budding of frustules, asexual reproduction by fissiparity, formation of propagules by fragmentation, encystment, polyp and medusa budding, asexual reproduction of medusae) as well as trans-differentiation and regeneration phenomena (Boero et al. 1997, 2002). In these processes, medusa formation from a planula can be viewed as an essentially embryological process interrupted (in its course) by an intense period of asexual reproduction through colony formation (Boero 2002). Furthermore, thermophilous species in favorable environmental conditions can take advantage of several asexual reproduction strategies like the direct budding of young medusae from marginal tentacular bulbs (Hyman 1940). The longitudinal division process (schizogony) proceeds via the formation of multiple stomach (polygastry) (Russell 1953) or by direct fission (Stretch & King 1980). These processes involve, when sexual reproduction takes place, an increase in density of mature medusae with the production of more widely dispersed sexual propagules.

It has been observed that Hydrozoa exhibit extreme sensitivity with respect to seasonal changes. Interestingly, there is a period in which no active hydroids are present, being the organism represented by resting hydrorhizae capable of tolerating substantial changes in temperature and drying conditions (Gili & Hughes 1995; Boero et al. 2002, 2008b; Bavestrello et al. 2006; Di Camillo et al. 2008 and references therein).

It is also important to highlight the difference between shallow and deep hydrozoan (and other organisms) populations. Seasonality of hydrozoan shallow water species is generally much more pronounced than those at greater depths because of stronger seasonal differences in temperature of surface coastal waters. The thermocline formation and differences in available food in summer time due to a lack of water movement or seston availability (see below) are one of the keys to understand shallow Hydrozoa life cycles (Coma et al. 2000). Hydroids below 20 m in the Mediterranean Sea, in fact, are characterized by more protracted spawning periods and longer-lived colonies (Boero 1984; Boero & Fresi 1986; Gili et al. 1989).

An emblematic case study is the cold-affinity species *Paracoryne huvei* Picard, 1957. This species is apparently present only in winter months whereas in the warmer period it forms cysts (Bouillon 1975): temperature seems to affect only the occurrence and length of the life cycle of this species while rainfall has effects on the settlement/development of the colonies (Betti et al. 2017b). Therefore, its strict stenothermic

feature and shortened life cycle (due to water warming and low salinity conditions) seem to make it suitable as bioindicator of climatic change (Betti et al. 2017b).

Many researchers have considered temperature to be the main factor responsible for the seasonal changes in the presence/abundance of different hydrozoan species (see papers of Kinne and Werner, listed in Gili & Hughes 1995). This hypothesis has been supported by laboratory experiments that have confirmed that hydroid colony growth is highest over a defined temperature range (Fulton 1962; Kinne & Paffenhöfer 1966; Gili & Hughes 1995). In Hydrozoa, in fact, temperature has been proved to play an important role in the processes of development and reproduction (see experiments on *Corynetubulosa* (M. Sars, 1835) conducted by Werner 1956, 1958, 1961): The results of these experiments showed that the internal conditions of metabolism, growth, and development influence the production of new stolons and polyps (as well as medusa buds), being regulated and initiated by temperature changes. *Rathkea octopunctata* (M. Sars, 1835) is another example of direct effect of temperature, in this case on cell determination; Werner (1958) showed that temperature could induce either medusa budding (at temperature $<7^{\circ}\text{C}$) or gametogenesis (at temperature $>10^{\circ}\text{C}$) in specimens collected in the North Sea. In the Mediterranean, *R. octopunctata* occurs in its budding asexual form at temperatures above the 13°C .

Sometimes, a lack of correspondence between the observed T values and the structural changes of the hydroid populations can be verified, as observed by Brock (1975, 1979), due to the presence of circannual clocks that contribute to regulate their activities (Boero & Fresi 1986). The circannual rhythms in Hydrozoa are defined by seasonal changes in growth of the colonies and in development and longevity of the hydranths (see case study of the species *Campanularia flexuosa*

(Alder, 1857) in Brock 1975): these observations highlight how the endogenous rhythms allow anticipation of seasonal variations in the natural environment.

Long time series are one of the clearer indicators of temperature shifts as a distribution driver in hydrozoans. In the Mediterranean Sea, over the last 50 years, the shallow water hydrozoan community displayed marked changes in species composition, bathymetric distribution, and reproductive timing, with increased dispersion and survival of species of warm-water affinity (including non-indigenous species) throughout the year (Bianchi & Morri 2003; Puce et al. 2009; Gravili et al. 2015a, 2015b; Gravili 2017; Martell et al. 2017) (Figure 1a,b). In particular, Puce et al. (2009) is the only study on hydroid communities in the Northern Mediterranean Sea demonstrating phenological changes linked to global warming across a 25-year period (from 1976 to 2004). About 70% of the cold-affinity hydroid species disappeared or were recorded in deeper areas (Puce et al. 2009). To our knowledge, this is one of the very few works in which invertebrate distribution in the Mediterranean Sea is related to temperature shifts.

Following the work by Boero and Fresi (1986) is evident that hydroids, due to their marked seasonality in temperate seas, are extremely sensitive to climatic changes and, therefore, the modifications observed in the phenology of hydroid assemblages must be considered in the evaluation of the impact of global warming on marine ecosystems. Furthermore, the regional species pool often remained stable in terms of species numbers but not in terms of species identity (Puce et al. 2009). This phenomenon is due to a combination of abiotic features and biotic interactions, favouring (native and non-indigenous) species of warm-water affinity with increased survival rate. The same trend is observed in the hydroid community of the Otranto Channel (years 2004–2005) (De Vito

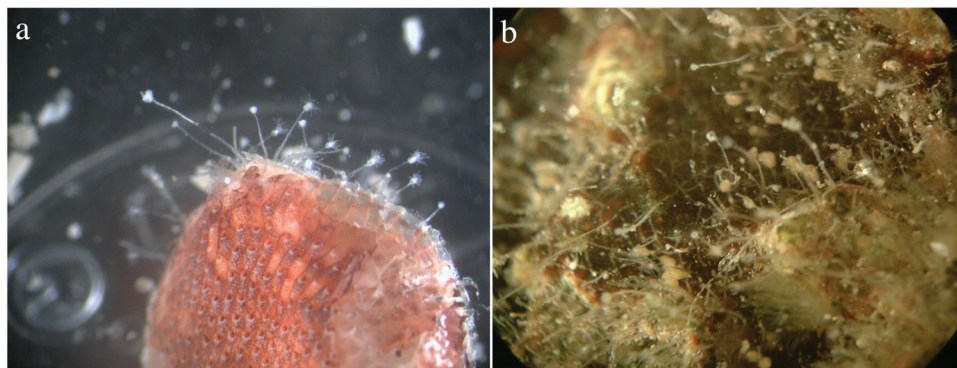


Figure 1. Non-indigenous hydrozoan *Clytia hummelincki* (Leloup, 1935) (Hydrozoa: Campanulariidae): (a) colony; (b) polyps and newborn medusa.

2006) where warm-affinity species have expanded their temporal distributions and reproduction into the cold season, compared to previous records from the whole Mediterranean Sea (Boero & Fresi 1986; Bouillon et al. 2004; Puce et al. 2009; Gravili et al. 2015b) (Figure 2a).

Conversely, temperate cold-affinity species either have disappeared altogether or became restricted in their bathymetric distribution to deeper areas, during shorter winter periods, showing a summer contraction of the occurrence of the polyp stage and/or of medusa or gonophore budding (De Vito 2006) (Figure 2b). Therefore, warmer waters and the enhanced stratification imply prolonged exposure to warmer summer conditions coupled with reduced food resources (Coma et al. 2009), conditioning the hydrozoan life cycles. The structural simplicity of

hydroids, together with the potential for cell re-differentiation and the presence of multipotent interstitial cells, allow alternative developmental patterns as responses to short-term environmental changes (Gili & Hughes 1995 and references therein; Schmich et al. 2007). A special process of propagation, the “autotomy phenomenon”, has been recorded for example in a few athecate species probably in response to changes in environmental factors, such as changes in temperature and oxygen concentration (Moore 1939; Berrill 1948; Tardent 1963, 1965; Rungger 1969 and references therein). Laboratory experiments with some hydroid species showed that temperature influences nutrition and food assimilation (Kinne 1957; Kinne & Paffenhöfer 1965; Paffenhöfer 1968) and the life-cycles of certain hydroids and hydromedusae (Moore 1939; Kinne 1956a, 1956b; Werner 1963 and references therein). It has been demonstrated in fact that temperature is a critical factor in stimulating or preventing hydroid reproduction (see papers of Berrill & Nishihira, listed in Gili & Hughes 1995; Hamond 1957; papers of Werner, listed in Jarms 1987; Kawamura & Kubota 2008). Several researchers (Boero et al. 1986; Arillo et al. 1989; Di Camillo et al. 2012) agree with a model of degenerative processes of populations of *Eudendrium glomeratum* Picard, 1952 and *E. racemosum* (Cavolini, 1785) not genetically predetermined but controlled by some environmental factors (among these, the temperature) as well as hydrozoan sex-determination (see the case studies of a few Hydrozoa genera such as *Clytia* and *Turritopsis*) dependent on environmental conditions with the dominance of males or females related to the sea water conditions (Carré & Carré 2000; Martell et al. 2016).

In Hydrozoa genetic sex determination is a labile character and is characterized by a remarkable plasticity (Carré & Carré 2000) with tendency of reaching sexual maturity at early stages with increasing temperatures (Piraino et al. 1996; Carlà et al. 2003; Martell et al. 2016). Even bud development can be altered by sudden changes in temperature (see Berrill 1953 for *Sarsia tubulosa* (M. Sars, 1835)). Temperature shifts may thus drive developmental watches of germ cells determination and differentiation, leading to seasonal, latitudinal or depth-dependent sex determination, as well as life-cycle inversion to maximize offspring production (Piraino et al. 2004).

The description of ontogeny reversal (a medusa that metamorphoses into a hydroid) in *Turritopsis dohrnii* (Weismann, 1883) under environmental

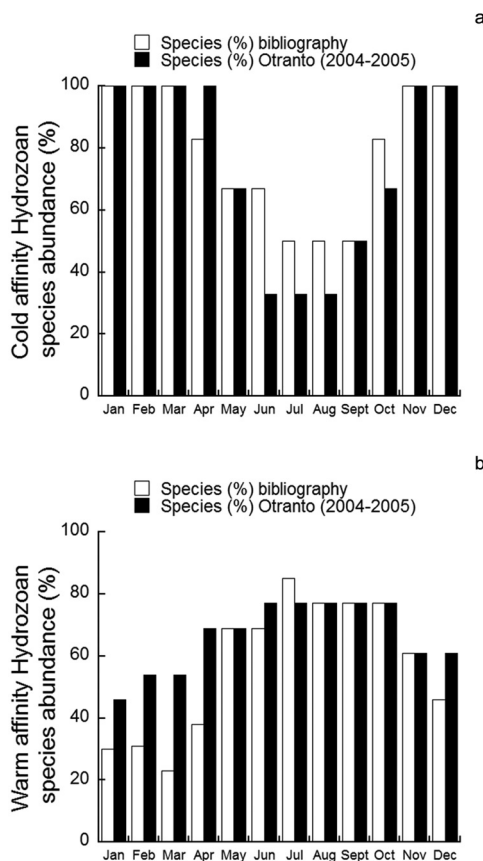


Figure 2. (a) Trend (temporal window range of the polyp stage and reproduction) of the hydrozoan community with cold-affinity species of the Otranto Channel (years 2004–2005). (b) Trend (temporal window range of the polyp stage and reproduction) of the hydrozoan community with warm-affinity species of the Otranto Channel (years 2004–2005) compared to previous records from the whole Mediterranean Sea.

stress (Piraino et al. 1996, 2004; Carlà et al. 2003; Martell et al. 2017) involves the contribution of trans-differentiation, I-cell-proliferation processes (Piraino et al. 1996), and the activation of cell-death programs (Carlà et al. 2003) confirming that development process must be considered “as an orchestration of both animal-encoded ontogeny and environmental interactions” (Bosch et al. 2014).

Scyphozoa

Many of the problematic bloom-forming cnidarian species are members of the class Scyphozoa. In the Mediterranean Sea, the most conspicuous and abundant jellyfish species belonging to this group are *Aurelia* spp., *Cotylorhiza tuberculata* (Macri, 1778), *Rhizostoma pulmo* (Macri, 1778) and the mauve stinger *Pelagia noctiluca* (Forsskål, 1775). The first three species count with a complex triphasic life cycle, consisting of a planula larva, an asexually reproducing benthic polyp and a pelagic ephyra/medusa stage (Hamner & Dawson 2009); on the other hand, *P. noctiluca* has a holoplanktonic life cycle, whose planula larva directly develops into the pelagic ephyra (i.e. without an intermediate polyp stage), and eventually into the adult medusa stage (Rottini Sandrini & Avian 1983).

Several studies focused on the effects and influence of different environmental factors on the metabolism and responses to seasonal cycles of pelagic jellyfish and benthic polyp stages (e.g. Morand et al. 1987; Youngbluth & Båmstedt 2001; Møller & Riisgård 2007; Lucas et al. 2012); especially in terms of periodic activities such as migration and reproduction (synchronising annual cycles of reproduction and influencing reproductive outputs) (Lucas 2001; Boero et al. 2016). Many jellyfish species, usually inhabiting coastal and shelf ecosystems, are tolerant of a wide range of environmental conditions (Arai 1997; Lucas 2001). Even if we have scarce information about the thermal preferences of the aforementioned species, their population increases suggest that they are able to take advantage of elevated temperatures, which probably lengthens their reproductive periods (Boero et al. 2016).

Seawater temperature, together with quantity and quality of available food resources, are known as major drivers of gonadal outputs (Stimson 1987; Harland et al. 1992; Ben-David-Zaslow & Benayahu 1999). Studies focused on *Aurelia* spp. jellyfish suggested that the restricted food availability limited the energy investment in sexual reproduction by the production of few, large planulae larvae,

while the well-fed medusae adopted an opportunistic strategy by producing many small planulae (Lucas & Lawes 1998). Temperature also affected specific growth and clearance rate of *Aurelia* ephyrae, which increase exponentially with this factor, but both, growth and clearance rates markedly decreased at high temperatures values (Møller & Riisgård 2007). Scyphozoans asexual reproduction would also be influenced by water warming. Some studies showed that elevated temperature by itself or in combination with high feeding frequency (due to raised zooplankton preys abundance) increased budding rate and bud size in *Aurelia* polyps populations worldwide (Willcox et al. 2007; Liu et al. 2009; Han & Uye 2010; Purcell et al. 2012; Sokołowski et al. 2016, and references therein). Equally, the process of strobilation in *Aurelia* has most frequently been correlated with changing temperature, irradiance and food supply, although no variable has been singled out as the major regulator (Lucas 2001; Purcell 2007; Holst 2012). Similar results have also been demonstrated in *Rhizostoma pulmo* and *Cotylorhiza tuberculata* (two of the most common Mediterranean native jellyfish species), presenting faster planulae settlement, increasing number of produced buds and new medusae (ephyrae) at higher temperatures (Kogovšek et al. 2010; Prieto et al. 2010; Astorga et al. 2012; Purcell et al. 2012; Ruiz et al. 2012).

Outbreaks of *Pelagia noctiluca*, the most abundant jellyfish in the Mediterranean Sea, seem to be associated with warmer winters and cold summers (Malej & Malej 2004; Rosa et al. 2013). In *P. noctiluca* the metabolism is directly proportional to the temperature oscillations (Rottini Sandrini & Avian 1983; Malej et al. 1986; Morand et al. 1987). A decrease in temperature causes decreasing swimming rates, a reduced capacity to find food and slower digestion times (Rottini Sandrini & Avian 1989; Giorgi et al. 1991). In contrast, temperature increase results in higher metabolism rates and greater food requirements. This would be in agreement with Rosa et al. (2013) who suggested that too high temperatures might have adverse effects on *P. noctiluca* populations in the Strait of Messina (Italy). Negative relationship between medusa abundance and temperature suggested that the exposure to high temperatures put *Pelagia* under an evident metabolic stress, disappearing at least from the surface layers. Lilley et al. (2014) proposed that vertical migration between day and night observed in this species (Ferraris et al. 2012) might be a strategy adopted to mitigate adverse temperature effects, especially in the warm season. Thus, when temperature becomes too high, specimens show a decrease

of activity (Rottini-Sandrini 1982) and jellyfish probably migrate vertically to deeper and colder water layers.

Swarms of this voracious zooplanktivore would be directly influenced by food availability and favourable environmental conditions (Rottini Sandrini & Avian 1991). Local-scale factors related to high primary production may lead to increased abundance of herbivorous crustacean prey and to higher *P. noctiluca* individual growth, as well as reproduction (Kogovšek et al. 2010) and population blooms (Boero 2013). Sexual reproduction requires a large investment of energy for the development of gonadal tissues and reproductive success directly depends on the amount of ingested food or on previously stored reserves (Fernández & Camacho 2005; Rossi et al. 2017). In this species, water temperature plays a key role in gonadal and oocyte development, growth, and gamete differentiation. Milisenda et al. (2018) observed that in the Strait of Sicily, *P. noctiluca* spawning events and egg fertilization occurred mainly in May and October, when the sea surface temperature was around 18–20°C. Fecundity Index and gonadosomatic index were used as indicators of spawning event, since a reduction of these indices with time suggests a release of mature eggs in the environment. Two different periods of decreasing fecundity index were identified: from April to July (mean temperature 19.5°C) and from September to December (mean temperature 20°C) (Figure 3). At this temperature, the time needed for planula metamorphosis into ephyrae is only 92 h, while at 13°C, metamorphosis may require up to 168 h (Avian & Rottini Sandrini 1991), thereby increasing the risk of mortality by predation (Avian 1986).

The female gonadal organic matter content may represent another useful proxy to understand reproductive dynamics of jellyfish, as a reflection of differential energy investments between somatic and gonadic tissues, which may fluctuate according to endogenous and environmental control mechanisms (e.g. food abundance and temperature) (Olive 1985). The content of organic matter (OM) in the female gonads of *P. noctiluca* was different in the two potential spawning periods. The highest gonadal OM value was recorded in late autumn, with poor quality and quantity of available zooplankton food (Ribera d'Alcalá et al. 2004); conversely, a low gonadal OM content was observed in spring, at the time of the highest food availability (Milisenda et al. 2018). Indeed, an increased amount of organic matter invested in the production of offspring may be considered as a strategy to ensure reproductive success under food shortage conditions (Olive 1985).

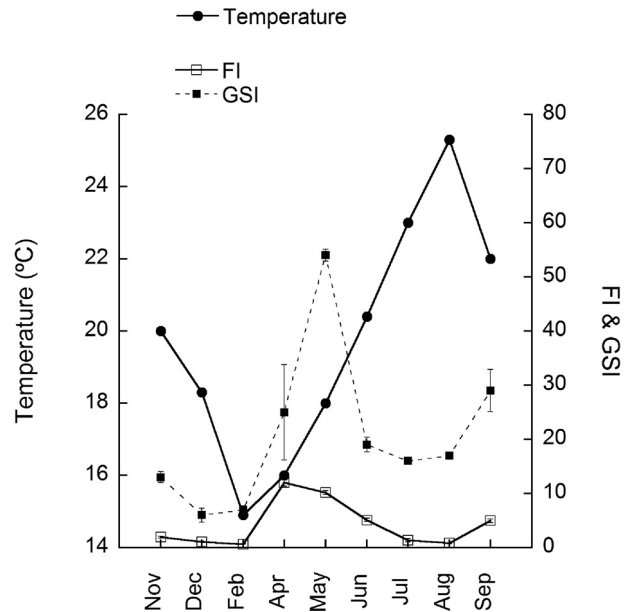


Figure 3. Temporal trend of gonadosomatic (GSI) and fecundity (FI) indexes for the scyphomedusae *Pelagia noctiluca* in the Strait of Messina (Italy). Together with sea surface temperature data are possible to observe two different periods of spawning: from April to July (mean sea surface temperature 19.5°C) and from September to December (mean sea surface temperature 20°C) from Milisenda et al. (2018).

Even if increasing temperature may impair jellyfish metabolism and, at the same time, may produce an ecosystem depletion, these organisms seem to be well adapted to survival in unfavourable conditions. The ability to produce resting stages, to modify the number and size of eggs or planulae to increase the ephyrae survivor probability, or to shrink for at least a month while still reproducing are different strategies that have to be considered in this complex framework (Larson 1987; Lucas & Lawes 1998; Milisenda et al. 2018). These characteristics may open up new ecological space for jellyfish in a future warmer environment, causing an increase in their spatiotemporal distribution that may affect Mediterranean ecological communities.

Anthozoa

Another group potentially affected in its reproductive traits by climate change in the Mediterranean Sea is the class Anthozoa. Benthic suspension feeders such as anthozoans depend on the water column production for feeding (Gili & Coma 1998). Quantity and quality of available food control the metabolism of these organisms (Coma et al. 1998;

Rossi et al. 2006a; Viladrich et al. 2017) and may affect their health status and biological functions (Rossi et al. 2017). The principal anthozoan groups in the Mediterranean benthos are the octocorals, such as gorgonians and alcyonarians (Sarà 1969; True 1970; Gili & Ros 1985; Ballesteros 2006). The main reproductive modes found in this group are internal or external brooding (Kahng et al. 2011), relying in both cases on lecithotrophic planula larvae for their dispersal (Fautin 2002). Internal brooders release larvae directly, whereas surface brooders and broadcast spawners release mature oocytes (for further external fertilization) or zygotes that will develop into planulae larvae (Kahng et al. 2011). The larval stage is a critical life phase with high mortality rates that forced the evolution of several strategies to increase survival (Strathmann 1985). Spawning triggers include environmental factors such as temperature, moon phases, day length, food availability, and tidal flux, among others. However, the synergy of these factors that ultimately prompts larval release is not completely understood (Harrison & Wallace 1998; Kahng et al. 2011; Crimaldi 2012; Heyward & Negri 2012).

Spawning takes place in late spring and summer in the studied octocoral species (e.g. *Alcyonium coralloides* (Pallas, 1766) in late spring; *Eunicella singularis* (Esper, 1791) and *Paramuricea clavata* (Risso, 1826) in late spring-early summer; *Alcyonium acaule* Marion, 1878, *Corallium rubrum* (Linnaeus, 1758) and *Leptogorgia sarmentosa* (Esper, 1789) in summer) (Coma et al. 1995; Tsounis et al. 2006; Gori et al. 2007, 2012; Ribes et al. 2007; Rossi & Gili 2009; Fiorillo et al. 2012; Quintanilla et al. 2013), in coincidence with its higher lipid contents (Figures 4 and 5). Previous studies showed similar spawning timing for some of these Mediterranean octocorals in other NW Mediterranean areas (Vighi 1972; Santangelo et al. 2003; Gori et al. 2007; Linares et al. 2008b), and other anthozoan species showed the same late spring-summer larval release *Leptosammia pruvoti* (Lacaze-Duthiers, 1897 (Goffredo et al. 2005), *Cladocora caespitosa* (Linnaeus, 1758) (Kruzic et al. 2008), *Caryophyllia inornata* (Duncan, 1878) (Goffredo et al. 2012)). Only in *Parazoanthus axinellae* (Schmidt, 1862) does spawning occur in late autumn, probably because it has a strong asexual component in its life-cycle evident in late summer time (Prelati et al. 2010a).

The phenomenon of lecithotrophic larvae released at the beginning or in the middle of the constraining summer phase appears counterintuitive, as the

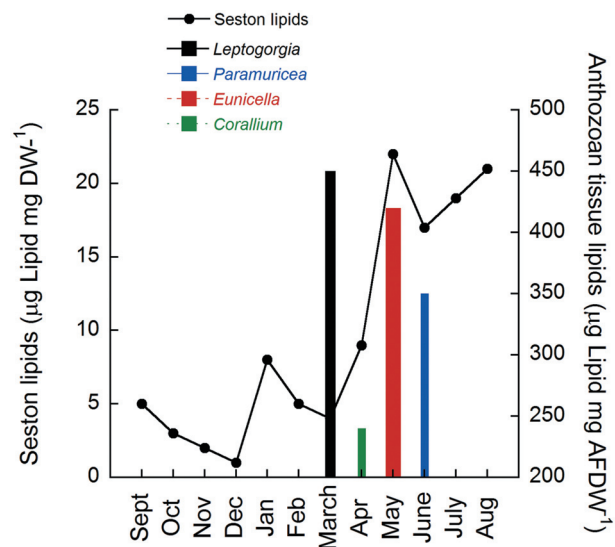


Figure 4. Four common species of octocorals (*Eunicella singularis*, *Paramuricea clavata*, *Leptogorgia sarmentosa*, *Corallium rubrum*) have their spawning period in late spring-early summer (from late May to early August). A higher water stratification and food depletion may affect their successful settlement: they depend on the environmental parameters and phytoplankton blooms of early autumn to face the first life stages. In the figure, the lipid maximum accumulation of mature colonies is in spring, when the lipids of the seston are abundant and, more important, available. In summer, the lipid concentration in the water column is high, but the particle concentration and the water movement low. Redrawn from Rossi et al. (2017).

Mediterranean summer is characterized by clear water, low plankton concentration and nutrient levels and seston scarcity (Estrada 1996; Rossi & Gili 2005). This is accompanied by high water temperatures in the surface, which results in high basal metabolic energy consumption especially in anthozoans (Coma et al. 2002; Rossi et al. 2006b; Prelati et al. 2010b). Transparent and warm waters contain low available food (Rossi & Gili 2005). These conditions of low food concentration and availability imply that adult colonies have to rely on energetic reserves, which are however, depleted after investing into reproduction (Coma et al. 1998; Rossi et al. 2006a; Gori et al. 2012). Thus, spawning and release of larvae in summer imply that lecithotrophic larvae of anthozoans settle and metamorphose few weeks before phytoplankton concentration rises in early fall (Estrada 1996; Rossi & Gili 2005; Siokou-Frangou et al. 2010), supplying moderate-high amounts of food. The fact that lecithotrophic larvae contain energy reserves that allow them to settle, metamorphose and also grow the first polyps without the need to feed (Benayahu & Loya 1984; Viladrich et al. 2016, 2017), suggests



Figure 5. Spawning of *Paramuricea*. This anthozoan is a surface brooder that invests most of its energy output in producing the female eggs that would be fertilized in a brief time-lapse.

that larvae might already have developed efficient feeding anatomical structures when food availability increases in autumn. Therefore, size and nutritional condition (i.e. energy stored) of lecithotrophic larvae might be a key factor to understand larval survival and thus recruitment, as well as new settlers mortality (Isomura & Nishihira 2001; Viladrich et al. 2017).

Spawning at the beginning and middle of the summer trophic constraints has further advantages. Larvae settle and metamorphose when algae (especially the fleshy ones, Ballesteros 1991) and other ephemeral suspension feeders (mainly hydrozoans and bryozoans, Boero 1984) clearly decline in its abundance and cover, avoiding trophic shadowing (Zabala & Ballesteros 1989; Coma et al. 2000). The settling and metamorphose of the larvae into the feeding polyp could thus be delayed from weeks to months (Weinberg & Weinberg 1979; Benayahu & Loya 1984), waiting for the appropriate moment or substrate to settle. Longevity and competence periods of the released larvae are related, among other things, to its energy content. The knowledge of initial amount of energy contained within a larva would thus allow estimation of the time-length elapse that metamorphosis can be delayed (Richmond 1987, 1988; Zaslow & Benayahu 2000; Martínez-Quintana et al. 2015).

After spawning, the Mediterranean anthozoans almost depleted such energy storage molecules (Rossi et al. 2006a; Rossi & Tsounis 2007; Gori et al. 2012; Viladrich et al. 2016, 2017). These observations agree with the expected physiological changes associated with a summer energy shortage

(reduced polyp activity, colony dormancy, low oxygen consumption, depletion of energy storage) and with an annual pattern of investment in growth and reproduction of the gorgonian species (Garrahou 1999; Coma et al. 2002; Rossi 2002; Rossi et al. 2006a). Regarding the Mediterranean species, we hypothesize therefore that larvae metamorphose and develop the first feeding polyp during late summer, thus being able to start feeding from late August to October (when the first signals of instability of the thermocline and the second peak of primary production in the Mediterranean sea occur, Estrada 1996; Ribera d'Alcalá et al. 2004; Rossi & Gili 2005). Recruits (and adults) will face a second trophic constraint in late autumn. In this period, the available food is very scarce due to the high hydrodynamism (resuspension) and the settling organic matter is of very low quality (Grémare et al. 1997, 2003; Rossi et al. 2003; see Figure 3). This food, with poor nutritive value, force the depletion of the energy stored (Rossi et al. 2006a, 2012; Rossi & Tsounis 2007) and stresses adult colonies (Rossi et al. 2006b), being probably a source of mortality for new recruits.

The described reproductive features and the larval release strategy of the studied octocorals species make them highly sensitive to global climate change (especially in shallow areas, above 40 meters depth). Recent models highlight that water stratification in the Mediterranean Sea may last for longer periods and warmer waters may stress non-mobile organisms (Galli et al. 2017). Doney et al. (2009) suggested that in warm and cold temperate seas, higher temperatures could revert in a stronger stratification of the water column, affecting phytoplankton dominance and productivity. In this sense, Smetacek and Cloern (2008) also suggested that in temperate coastal areas, secondary production in pelagic ecosystems is already changing, affecting the potential quality of food transferred to other organisms. Whether the food availability for benthic suspension feeders would be affected by elevated temperatures is not clear, but it has been shown that under anomalous warming episodes in shallow water adults of *P. clavata*, *E. singularis* and *C. rubrum* suffer from partial or total tissue loss (Garrahou et al. 2001; Linares et al. 2005, 2008a; Rossi & Tsounis 2007). Also the new recruit mortality in shallow populations is very high when compared to deeper populations (Bramanti et al. 2005; Coma et al. 2006; Linares et al. 2008a). Viladrich et al. (2016), Viladrich et al. (2017) showed that mother care (i.e. the energy invested by mother

gorgonian colonies to the offspring) will be crucial to understand the potential survival in a warmer and less productive oceans. Within the context of global change, there is a risk that the period of trophic crisis might be significantly prolonged to the point that the capacity of the energy reserves in lecithotrophic larvae would not last until the arrival of favourable feeding conditions in early autumn. This situation could be even worse if the spawning of these species would be triggered earlier by the increase in temperature. Asexual reproduction may enable some individuals to survive catastrophic mortality events such as warming episodes and then expand following the perturbation (Lasker & Coffroth 1999). However, chronic stress that reduces recruitment will have less obvious effects on these clonal taxa and may be the key to understand future composition of benthic communities. Climate change could lead to partial recruitment failure in the affected species, with major changes in the population structure and dynamics, and a drastic change in the ecosystem functioning. These combined factors may be crucial to understand how seascape will change in shallow Mediterranean benthic communities.

Conclusions

Looking at the different seawater warming impacts on reproductive traits in cnidarians, it seems that several species will change its distribution patterns during the next decades. The deficiency or total lack of time data series constitute an obstacle to understanding the biological response to climate change in the Mediterranean (Bianchi 1997; Bianchi & Morri 2004; Bianchi et al. 2018), giving little chance to make a clear picture of what is really happening with hydrozoans, scyphozoans and anthozoans. However, some cues can be envisaged. The most affected populations will be, in a midterm, those living in shallow waters. The sea surface warming, responsible for massive mortalities due to a prolonged high-temperature situation (Garrahou et al. 2009), is already shaping the new seascape. Temperature, but also water stratification and changes in the energy storage capability, will be key factors to understand reproductive trends in organisms that are used to live in a warm temperate sea upon certain primary-productivity conditions. Understanding the reproductive cycles and the potential dispersion of cnidarians in the Mediterranean Sea will be essential if we want to have a clear idea of what will happen at the level of trophic ecology, species

interaction and future ecosystem functioning in this warm temperate sea that is in a transitional state.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Marie Curie International Outgoing Fellowship (ANIMAL FOREST HEALTH, Grant Agreement Number 327845) and P-SPHERE (COFUND Marie Curie, Grant Agreement Number 665919).

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