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IS GLOBAL WARMING INVOLVED IN THE SUCCESS OF SEAWEED INTRODUCTIONS IN THE MEDITERRANEAN SEA?

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1. Introduction

There is growing concern about the global warming of the Earth and about introduced species (biological invasions) (e.g. Stott et al., 2000; Oreskes, 2004; Schaffelke et al., 2006). The reasons are: (i) Both warming and biological invasions are not only in progress but are on the increase. (ii) They are more or less irreversible phenomena at human scale. In contrast, some other human impacts such as domestic pollution and oil spills are not only reversible, but also often on the decrease (Table 1; Boudouresque et al., 2005). (iii) The ecological and economic impact is huge (Pimentel et al., 2001; Boudouresque, 2002a; Goreau et al., 2005; Kerr, 2006; Sala and Knowlton, 2006), though often underestimated by stakeholders.

Politicians, decision-makers and civil servants at the ministries of the environment are often inclined to make a cause and effect connection between climate warming and the increasing rate of species introductions. Be the aim conscious or unconscious, it is not purely a matter of chance. As long as we are not able to control carbon dioxide and other greenhouse gas emissions, species introductions will be impossible to prevent. Therefore, the fact that they do not implement the international conventions they have ratified, aimed at preventing and combating species introduction, is of no importance. It is worth noting that most European countries and all Mediterranean ones have not yet drafted a single text of law to apply the recommendations of the international conventions dealing with species introduction (Boudouresque, 2002b; Boudouresque and Verlaque, 2005).

Some scientific papers also envisage, explicitly or not, a cause and effect link between climate warming and the success of biological invasions (e.g. Dukes and Mooney, 1999; Bianchi, 2007; Galil et al., 2007; Occhipinti-Ambrogi, 2007; Galil, 2008; Hellmann et al., 2008; Perez, 2008). However, they usually do not present accurate data supporting the assumption, or they only present partial and therefore possibly biased data.

The goal of this study is to revisit the possible link between climate warming and the growing flow of species introductions, their biogeographical origin and

Table 1. Time needed for recovery, after the end of the forcing disturbance.

Disturbance	Human origin?	Natural origin?	Recovery	Key references
Domestic pollution (soft substrates)	+	−	<1–10 a	Bellan et al. (1999)
Artisanal fishing (fish abundance)	+	−	<5–10 a	Ramos (1992); Roberts et al. (2001)
Oil spill	+	−	<10 a	Raffin et al. (1991)
Disease of marine species	±	+	>10 a	Moses and Bonem (2001)
Loss of long-lived species	+	±	10–100 a	Soltan et al. (2001)
Coastal development	+	−	Millennia	Meinesz et al. (1991)
Over-fishing (genetic change)	+	−	Millennia?	Conover (2000); Law (2000); Kenchington et al. (2003); Olsen et al. (2004); Jørgensen et al. (2007)
Climate warming	+	+	Glacial cycle?	Zwiers and Weaver (2000); Barnett et al. (2001)
Biological invasions	+	−	Irreversible	Bright (1998); Clout (1998)
Species neo-extinction	+	−	Irreversible	Carlton (1993); Powles et al. (2000)

their success. Here, we shall only consider the seaweeds, a polyphyletic set of multicellular photosynthetic organisms (MPOs) belonging to the Chlorobionta, Rhodobionta (kingdom Plantae) and Phaeophyceae (kingdom Stramenopiles) (Boudouresque et al., 2006; Lecointre and Le Guyader, 2006) and the Mediterranean Sea, a set of taxa and an area for which an exhaustive data set is available (Verlaque et al., 2007b).

2. Climate Change and Global Warming

Since the birth of the planet Earth, 4,560–4,540 Ma (million years) ago (Jacobsen, 2003), its climate has never stopped changing. Over the past 50 Ma, the Earth's climate has been steadily cooling. Large ice sheets appeared in the Northern Hemisphere 2.7 Ma ago (Billups, 2005). Since then, the climate has fluctuated between glacial and interglacial episodes (glacial cycles); about 850,000 years ago, the period of the glacial cycles changed from 41,000 to 100,000 years (de Garidel-Thoron et al., 2005). Glacial cycles break down into 5,000–10,000 years and ~1,500 years cycles (Cacho et al., 2002; Braun et al., 2005; Sachs and Anderson, 2005). As a rule, all these cycles are characterised by slow cooling and abrupt warming (Tabeaud, 2002; Leipe et al., 2008).

The last cold maximum of a glacial cycle (LGM, Last Glacial Maximum) occurred 21,000 years ago (Berger, 1996; Tzedakis et al., 1997). Within the current interglacial episode, the last cold maximum of a 1,500-year cycle is known as the

Little Ice Age (LIA). It peaked from the thirteenth to the early nineteenth century (Le Roy-Ladurie, 2004). The sea surface temperature conspicuously dropped (deMenocal et al., 2000), which probably favoured the Southward expansion of cold resistant species. The subsequent rapid warming, from the mid-nineteenth century, should have driven a reverse effect, i.e., a dramatic regression of cold-water affinity species and better conditions for warm-water species. Obviously, the present-day release of greenhouse gas due to human activity should have enhanced these natural trends from 1970 onwards (Stott et al., 2000; Oreskes, 2004).

Taking 1900 as the baseline, in the Mediterranean, there has been a sea-surface temperature (SST) increase of 0.2°C in the Eastern basin and 1°C in the Western basin (Moron, 2003). Since 1974, in Catalonia (Spain), the increase is 1.1°C for SST and 0.7°C at 80 m depth (Salat and Pascual, 2002). However, taking 1856 as the baseline, there is no clear trend of SST increase at Mediterranean scale. These apparent mismatches are due to the occurrence of multidecadal cycles. In the Mediterranean Sea, the temperature (SST) was relatively higher in 1875–1880, 1935–1945 and in the 2000s than around 1860, 1905–1910 and 1975–1980; the 1935–1945 warming (+0.2–0.7°C) was more pronounced in the Eastern than in the Western basin, whereas the opposite is the case for that of the 2000s (Moron, 2003). Locally, the peaks can shift to a greater or lesser degree; for example, at Marseilles (France), for the 1885 to 1967 period, SST peaked in the 1890s and 1930s–1940s (Romano and Lugrezi, 2007).

3. Introduction of Seaweed Species

An introduced species is defined here as a species, which fulfils the four following criteria (Boudouresque and Verlaque, 2002a). (i) It colonises a new area where it did not previously occur. (ii) There is geographical discontinuity between its native area and the new area (remote dispersal). This means that the occasional advance of a species at the frontiers of its native range (marginal dispersal) is not taken into consideration. Such fluctuations (advances or withdrawals) may be linked to climatic episodes. (iii) The extension of its range is linked, directly or indirectly, to human activity. (iv) Finally, new generations of the non-native species are born in situ without human assistance, thus constituting self-sustaining populations: the species is established, i.e., naturalised.

In the marine realm, the main vectors of introduction are fouling and clinging on ship hulls, solid ballast (up to the late-nineteenth century), ballast water, fishing bait, escape from aquariums, waterways and canals crossing watersheds, transoceanic canals such as the Suez Canal, aquaculture and even scientific research (Por, 1978; Zibrowius, 1991; Carlton and Geller, 1993; Verlaque, 1994; Ribera and Boudouresque, 1995; Boudouresque, 1999a; Boudouresque and Verlaque, 2002b; Olenin, 2002; Galil et al., 2007). As far as aquaculture is concerned, the introduction can occur through escape of reared and cultivated species from sea farms and from the transport of reared species, such as fish and molluscs, from one aquaculture basin to another distant one, with all the accompanying species (e.g. parasites and epibiota); when the recipient habitats are suitable, these species can survive and become established, resulting in unintentional introductions (Verlaque et al., 2007a). In the Eastern Mediterranean, the Suez Canal, which connects the Red Sea to the Levantine Basin, constitutes the main vector of species introduction. In contrast, in the Western Mediterranean, the main vector is aquaculture (Galil, 2008; Galil, 2009).

The Mediterranean is one of the areas worldwide most severely hit by biological invasions, with about 600 introduced species of MPOs and Metazoa (Boudouresque et al., 2005; Galil et al., 2007; Galil, 2008; Zenetos et al., 2008; Galil, 2009).

As far as seaweeds are concerned, 106 species were probably introduced into the Mediterranean (Table 2; Fig. 1). This is a conservative value: (i) Possible cryptogenic introductions (sensu Carlton, 1996) are not taken into account; these are species whose extensive range area might be the result of ancient introduction events, before the first inventories in the area, and whose native region (within the current area) remains unknown; they are therefore classified as native by default. (ii) In the same way, species considered as native could prove to be cryptic introductions; these are species closely resembling a native one; identification of their possibly exotic status would require an in-depth study; several species in Table 2 were at first considered as native until on the basis of a genetic study, they were assigned to a sibling exotic taxon. (iii) The introduction of exotic strains of species already present in the Mediterranean (gene introduction), e.g., *Cladosiphon zosterae*, *Desmarestia viridis*, *Ectocarpus siliculosus* var. *hiemalis* and *Pylaiella littoralis*, has not been taken into consideration here.

Since the beginning of the twentieth century, the number of seaweeds introduced into the Mediterranean has more or less doubled every 20 years (Ribera and Boudouresque, 1995; Boudouresque, 1999a; Verlaque and Boudouresque, 2004; Boudouresque et al., 2005). A similar steady increase over time has occurred for Mediterranean Metazoa (Boudouresque, 1999b; Galil, 2008), e.g., mollusc species (Zenetos et al., 2003) and in other areas, e.g., in the Bay of San Francisco (Cohen and Carlton, 1998). However, in the Mediterranean, the post-2000 increase does not fit the previous trend (Fig. 1); the possibility that the number of introduced seaweeds is reaching a plateau must be considered (see below).

4. The Relationship Between Seaweed Introduction and Climate Warming

4.1. MORE SPECIES?

The increase in the number of introduced species is clearly parallel to the twentieth century SST increase. However, as pointed out by Galil (2008), concurrent phenomena do not in themselves imply causation. This increase is parallel to that

Table 2. Seaweeds introduced into the Mediterranean. The date of first observation is the date of publication when no more information is available. For seaweed authorities, see Guiry and Guiry (2008).

Species	Date of first observation	Probability of introduction	Probable vector of introduction	Probable geographical origin	Native biogeographical distribution
Rhodobionta (Plantae)					
Acanthophora nayadiformis	1798–1801	H	?	RS, IP	Tr
Acrochaetium codicola	1952	V	FO, O	IP	NT
Acrochaetium robustum	1944	H	S	IP	NT, Tr
Acrochaetium spathoglossi	1944	H	S	IP	Tr
Acrochaetium subseriatum	1944	H	S	IP	Tr
Acrothamnion preissii	1969	V	FO	IP	NT, Tr, ST
Agardhiella subulata	1984	H	O	A	NT, Tr
Aglaothamnion feldmanniae	1975	M	FO	A	NT
Ahnfeltiopsis flabelliformis	1994	V	O	J	NC, NT, Tr
Anotrichium okamurae	?	M	FO	?	NT
Antithamnion amphigeneum	1989	V	FO	P	ST
Antithamnion nipponicum	1988	V	O	P	NC
Antithamnionella boergesenii	1937	M	?	?	NT, Tr
Antithamnionella elegans	1882	V	FO	J	Tr
Antithamnionella spirographidis	1911	H	FO	IP	NC, SC
Antithamnionella sublittoralis	1980	H	FO	IP	NT
Antithamnionella ternifolia	1926	V	FO	SH	NC, SC
Apoglossum gregarium	1992	M	FO	IP?	Tr
Asparagopsis armata	1880	V	FO	IP	ST, SC
Asparagopsis taxiformis sp. 1	1798–1801	H	S, FO	A	NT, Tr
Asparagopsis taxiformis sp. 2 invasive	1996	H	FO?	IP	ST
Bonnemaisonia hamifera	1909	V	FO	IP	NC, NT
Botryocladia madagascarensis	1991	H	FO?	IP	Tr
Ceramium bisporum	1980	M	FO	A	Tr
Ceramium strobiliforme	1991	H	FO?	A	Tr
Chondria coerulescens	1995	V	O	A	NT
Chondria curvilineata	1981	H	FO	A	NT, Tr
Chondria pygmaea	1974	V	S	RS	Tr
Chondrus giganteus f. *flabellatus*	1994	V	O	J	NC
Chrysymenia wrightii	1978	V	O	J	NC
Dasya sessilis	1984	V	O	J	NC
Dasysiphonia sp.	1998	V	O	P	NC
Feldmannophycus okamurae	1937	H	FO	IP	NC, NT, Tr
Galaxaura rugosa	1990	V	S	RS	Tr
Ganonema farinosa	1808	M	S	RS	NT, Tr, ST

(continued)

Table 2. (continued)

Species	Date of first observation	Probability of introduction	Probable vector of introduction	Probable geographical origin	Native biogeographical distribution
Goniotrichopsis sublittoralis	1989	H	FO	IP	NC, NT
Gracilaria arcuata	1931	H	S	RS, IP	Tr
Grateloupia asiatica	1984	V	O	IP	NC, NT
Grateloupia lanceolata	1982	V	O	J	NT
Grateloupia patens	1994	V	O	J	NC, NT
Grateloupia subpectinata	1997	H	O	IP	NC, SC
Grateloupia turuturu	1982	V	O	J	NC
Griffithsia corallinoides	1964	H	O	A	NC, NT
Herposiphonia parca	1997	V	O	IP	NT, Tr
Hypnea cornuta	1894	H	S	RS	NT, Tr
Hypnea flagelliformis	1956	H	S	IP	NT, Tr
Hypnea spinella	1928	H	FO?	PT	NT, Tr, ST
Hypnea valentiae	1996	H	S, FO	RS	NT, Tr, ST
Laurencia caduciramulosa	1991	M	FO	?	Tr
Laurencia okamurae	1984	H	O	P	NT, Tr
Lithophyllum yessoense	1994	V	O	P	NC
Lomentaria hakodatensis	1978	V	O	J	NC, NT, Tr
Lophocladia lallemandii	1908	M	S, FO	RS	NT, Tr
Nemalion vermiculare	2005	V	O	IP	NC
Nitophyllum stellato-corticatum	1984	V	O	J	NT
Pleonosporium caribaeum	1974	M	FO, O	PT	Tr
Plocamium secundatum	1976	M	?	SH	SC
Polysiphonia atlantica	1969–1971	H	O, FO	A	NT
Polysiphonia fucoides	1988	H	FB	A	NC, NT
Polysiphonia harveyi	1958	V	FO?	IP, A	NC, NT
Polysiphonia morrowii	1997	V	O	P	NC
Polysiphonia paniculata	1967	H	?	P	NC, NT, ST
Porphyra yezoensis	1975	V	O	J	NC
Pterosiphonia tanakae	1993	V	O	J	NT
Rhodophysema georgii	1978	H	O	A	NC, NT
Rhodymenia erythraea	1948	V	S, FO	RS, IP	Tr
Sarconema filiforme	1944	V	S	RS	Tr
Sarconema scinaioides	1945	V	S	IP	Tr
Solieria dura	1944	V	S	RS	Tr
Solieria filiformis	1922	M	?	A	NT, Tr
Symphyocladia marchantioides	1984	V	FO	IP	NC, NT, Tr, ST, SC
Womersleyella setacea	1986	V	FO	PT	Tr
Chlorobionta (Plantae)					
Caulerpa mexicana	1939	V	S	RS	NT, Tr
Caulerpa racemosa var. *cylindracea*	1990	V	AQ, BW	IP	ST
Caulerpa racemosa var. *lamourouxii*	1951	M	S	RS	Tr
Caulerpa racemosa var. *turbinata*	1926	M	S	RS	Tr

(continued)

Table 2. (continued)

Species	Date of first observation	Probability of introduction	Probable vector of introduction	Probable geographical origin	Native biogeographical distribution
Caulerpa scalpelliformis	1929	H	S	RS	Tr
Caulerpa taxifolia MAAS[a]	1984	V	AQ	PT	ST
Cladophora herpestica	1948	V	S	RS	NT, Tr, ST
Cladophora patentiramea	1991	H	S, FO	IP	Tr
Codium fragile subsp. *tomentosoides*	1946	V	FO, O	IP	NT
Codium taylori	1955	M	FO?	A	NT, Tr
Derbesia boergesenii	1972	H	S	RS	Tr
Derbesia rhizophora	1984	V	O	J	NT
Neomeris annulata	2003	H	S	RS	Tr
Ulva fasciata	1979–1984	H	O	J	NT, Tr, ST
Ulva pertusa	1984	V	O	IP	NT, Tr
Ulvaria obscura	1985	H	O	A	NC, NT
Phaeophyceae (Stramenopiles)					
Acrothrix fragilis	1998	H	O	A, P	NC
Botrytella parva	1996	H	?	?	NC
Chorda filum	1981	V	O	A, J	NC, NT
Colpomenia peregrina	1918	V	FO	IP	NC, NT, ST, SC
Fucus spiralis	1987	V	FB	A	NC, NT
Halothrix lumbricalis	1985	H	O	?	NC, NT
Leathesia difformis	(1905) 1979	H	O	A	NC, NT, ST, SC
Padina boergesenii	1962–1965	H	S	RS	Tr
Padina boryana	1974	V	S	IP	NT, Tr
Punctaria tenuissima	1985	H	O	A	NC, NT
Rugulopterix okamurae	2002	V	O	J	NT, Tr
Saccharina japonica	1976	V	O	J	NC, NT
Sargassum muticum	1980	V	O	J	NC
Scytosiphon dotyi	1960–1977	V	O	P	NT
Spathoglossum variabile	1944	V	S	RS	Tr
Sphaerotrichia firma	1970	H	O	J	NC
Stypopodium schimperi	1973?	V	S	RS	Tr
Undaria pinnatifida	1971	V	O	J	NT

Probability of introduction: V = very high, H = high, M = medium. Vector of introduction: AQ = aquariums, BW = ballast water, FB = fishing baits, FO = fouling on ship hulls, O = oyster culture, S = Suez Canal (Lessepsian species). Geographical origin: A = Atlantic, BS = Black Sea, IP = Indo-Pacific, J = Japan, P = Pacific, PT = pan-tropical, RS = Red Sea, SH = Southern hemisphere. Native biogéographical distribution: NC = North cold, NT = North temperate, Tr = tropical, ST = South temperate, SC = South cold (see caption to Table 3).
a MAAS = Mediterranean Aquarium and Australian Strain.

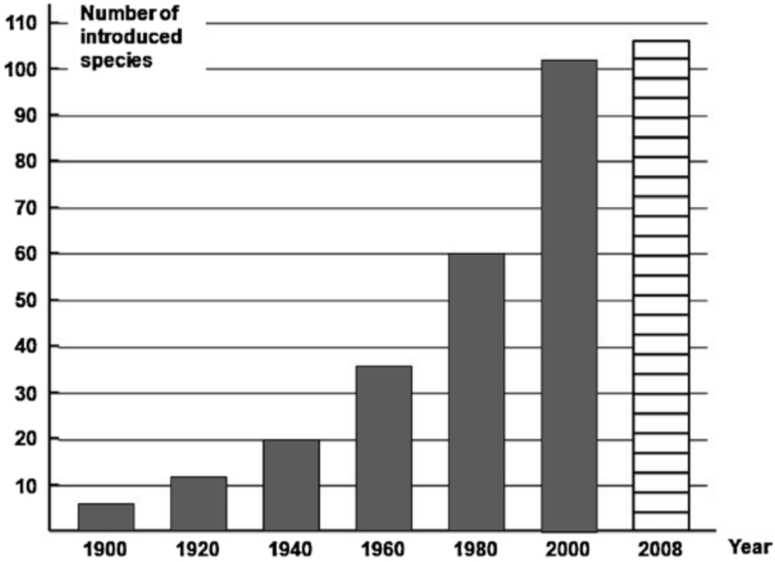

Figure 1. The cumulative number of seaweeds introduced into the Mediterranean Sea and its increase over time. Hatching for the 2008 value means that it does not correspond to the same 20-year time interval as the other values.

of the demographic pressure (Benoit and Comeau, 2005), that of the forest surface area in Western Europe and to the surge in highway traffic as well.

In fact, the increase in the number of introduced species is more probably related to the strengthening of the vectors: more aquaculture, more pleasure boats, more trade, more ships, more voyages, more speed, etc. (see Dobler, 2002; Benoit and Comeau, 2005; Briand, 2007).

4.2. MORE TROPICAL SPECIES?

Unexpectedly, the importance of tropical regions as donor areas for introductions of seaweeds to the Mediterranean was conspicuously higher in the 1800–1940 and 1941–1980 periods than later on, whereas the importance of both Southern and Northern cold regions increased from the 1980s (Table 3). Two factors, which are not mutually exclusive, may account for this. (i) Up to the 1950s, Lessepsian species, i.e., Red Sea species entering the Mediterranean via the Suez Canal, constituted the bulk of the seaweeds introduced into the Mediterranean. The Red Sea is a tropical realm. The number of new Lessepsian species peaked in the 1941–1950 period (Fig. 2), perhaps in relation with the gradual disappearance of the high-salinity barrier constituted by the Bitter Lakes up to the 1950s (see Por, 1978, 1989;

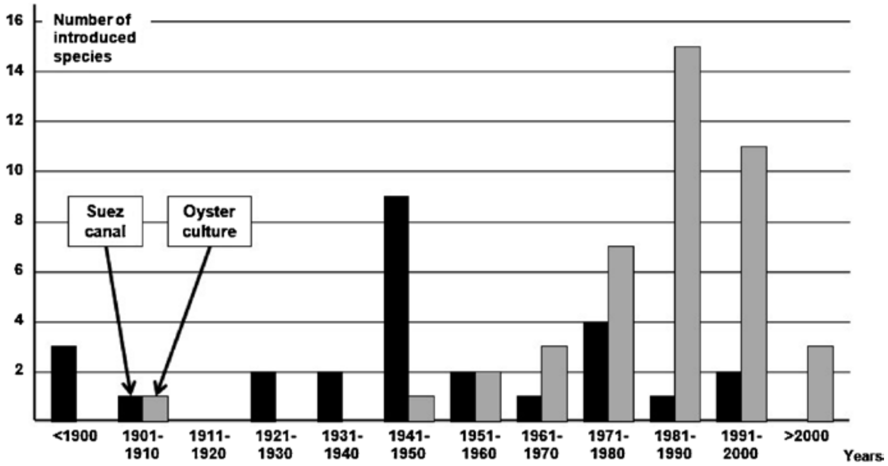

Figure 2. The number of seaweeds introduced into the Mediterranean per 10-year period (with the exception of <1900 and >2000). Two vectors are taken into account: the Suez Canal and oyster culture.

Boudouresque, 1999b). Subsequently, oyster culture took over from the Suez Canal as the main vector (Fig. 2). Massive importations of *Crassostrea gigas* oyster spat and adults from the Northern Pacific (mainly Japan), without either decontamination or quarantine, occurred in the 1970s; illegal importations (from Korea), in lesser amounts, continued up to the early 1990s (Grizel and Héral, 1991; Verlaque, 2001; Boudouresque and Verlaque, 2002b; Verlaque et al., 2007a). Donor regions were located in a cold biogeographical province. The shift from mainly tropical towards mainly cold-affinity introduced species can therefore be related to a change in the prevailing vector and the donor region. (ii) It might have been reasonable to suspect that the location of the Mediterranean phycologists changed over time, leading to phycologists working now in the Western basin rather than in the Eastern, which may have resulted in a distortion; oyster importations from cold waters of the Northwestern Pacific actually occurred mainly in Western Europe. In fact, this is the exact opposite of what actually occurred, the number of phycologists rather increasing in Eastern Mediterranean countries whereas declining in the Western ones.

If we remove the vector effect, which obviously accounts for the current biogeographical origin of most introduced species, a warmer Mediterranean should be more welcoming for a tropical than for a cold-water candidate species, and make easier its establishment. However, at the same time, cold-water candidates might be disadvantaged, so that the overall amount of new introduced species would be unchanged.

The assumption that most of the introduced species in the Mediterranean are thermophilic, originating in tropical seas (Galil, 2008; Galil, 2009), may prove to be true for Metazoa (kingdom Opisthokonts), but absolutely not for the MPOs belonging to the kingdoms Plantae and Stramenopiles. The media coverage of some introduced species believed to be of tropical origin, when they actually originate in temperate sea, has probably contributed to misleading authors. *Caulerpa taxifolia* is probably a complex of cryptic species mostly thriving in tropical seas. When it burst in on the Mediterranean, the media and scientists referred to it as 'the tropical alga' (Meinesz and Hesse, 1991; Boudouresque et al., 1995). Subsequently, molecular studies revealed the geographical origin of the strain (Mediterranean Aquarium and Australian Strain (MAAS) see Table 2): temperate Southeastern Australia (Jousson et al., 1998, 2000; Meusnier et al., 2001). Similarly, *Caulerpa racemosa* probably encompasses a complex of cryptic species. When discovered in the Mediterranean, *C. racemosa* var. *cylindracea* was at first confused with a tropical taxon already introduced into the Mediterranean, *C. racemosa* var. *turbinata* (e.g. Nizamuddin, 1991; Djellouli, 2000; Buia et al., 2001). Its true status and native area, temperate Southwestern Australia, was rapidly established (Verlaque et al., 2000, 2003). Finally, the invasive strain of *Asparagopsis taxiformis* (in fact a distinct species), which closely resembles a species common in the tropical Atlantic Ocean, actually comes from a Southern Australian temperate area (Ní Chualáin et al., 2004; Andreakis et al., 2007).

4.3. ARE THE INTRODUCED SPECIES MORE AGGRESSIVE?

As pointed out by Occhipinti-Ambrogi (2007), climate warming alters the competitive interactions between introduced and native species.

Once introduced, warm-water species (either of tropical or subtropical origin) should benefit from a warming Mediterranean (Galil, 2009). Roughly, SST is higher in the East and South than in the West and North. The current expansion of their area, Westwards and Northwards, has actually been observed (Galil, 2008). However, whatever the temperature trend, the marginal spread of an introduced species from its site of arrival constitutes a normal feature: it aims to occupy the whole of the suitable habitats and area. This spread can be very rapid, as occurred with the Chlorobionta *Caulerpa racemosa* var. *cylindracea*, which colonised the whole Mediterranean and the adjacent Atlantic coasts in less than 15 years (Verlaque et al., 2004). This spread can also take more time, as for the crustacean *Metapenaeus monoceros* (Fabricius 1798) and the fishes *Siganus luridus* (Rüppel 1829) and *S. rivulatus* (Forsskål 1775), which took 6 to 8 decades to spread from the Levant to Tunisia and Sicily (Galil, 2008). The natural marginal spread and the possible enhancement of the spread due to the SST warming are superimposed, so that unravelling their respective roles is not easy; it is therefore to be feared that premature conclusions are often drawn (i.e. 'the westwards spread of an introduced thermophilic species is due to the SST warming'). Be that as it may, it is worth noting that the current spread of native thermophilic species, such as the fishes *Sparisoma cretense* (Linnaeus 1758) and *Thalassoma pavo* (Linnaeus 1758) and the scleractinian coral *Astroides calycularis* (Pallas 1767) proves that the warming matters, whatever the degree of its contribution (Francour et al., 1994; Morri and Bianchi, 2001; Bianchi and Morri, 2004; Bianchi, 2007).

Whereas some warm-water introduced species advance, maybe partly in relation with the SST increase, such as the Rhodobionta *Womersleyella setacea* and the Phaeophyceae *Stypopodium schimperi*, the decline in abundance and the shrinking of the range of cold-water species, such as the Rhodobionta *Asparagopsis armata* (gametogenic phase) and the Chlorobionta *Codium fragile*, may be expected. Unfortunately, no data are available for the latter process: the arrival of a species at a new locality attracts more attention (and results in a scientific paper) than its absence from a previously occupied site (which may be thought to be temporary). Similarly, in the continental realm, Dukes and Mooney (1999) emphasised the components of global change (e.g. climate warming) likely to favour biological invaders, but did not consider those species, which could be disadvantaged.

Can we consider that '[algae] that are gaining ascendancy [in Mediterranean coastal ecosystems] are of tropical origin', as argued by Bianchi (2007)? Among the three seaweeds cited by the author in support of his assertion (*Stypopodium schimperi*, *Caulerpa taxifolia* and *C. racemosa* var. *cylindracea*), only the first one is actually of tropical origin.

4.4. WHAT COULD DEMONSTRATE THE IMPACT OF WARMING?

How could the impact of warming, either qualitative (which species?) or quantitative (how many species? How invasive?), on seaweed introductions, be demonstrated? (i) The increase in the number of introduced species reflects the nature and the strength of the vectors and is therefore irrelevant (see Section 4.1). (ii) The crossing of the limits of the potential area the species can occupy, a function of its physiology and competitive ability, would constitute a good criterion for a thermophilic species. However, this potential area is unknown. In addition, the spread of an introduced species is often a slow process, which takes decades, so that for many species, it may be suspected that they have not yet occupied their full potential area. Por (1989, 1990) delimited the 'Lessepsian province' corresponding to the potential expansion area of the Lessepsian species. At the moment, no strictly Lessepsian seaweeds have been reported outside this area, although a Magnoliophyta (Plantae), *Halophila stipulacea* (Forsskål) Ascherson, and several Metazoa have passed this limit. (iii) The resumption of the spread after a period of relative stasis was indicative that the potential area was reached. Four species of putatively thermophilic seaweeds might seem to meet this criterion: *Asparagopsis taxiformis*, *Caulerpa racemosa*, *Ulva fasciata* and *Lophocladia lallemandii*. The first two species proved to result in fact of new introduction events, i.e., the introduction of distinct taxa of temperate affinity, namely *Asparagopsis taxiformis* sp. 2 and *Caulerpa racemosa* var. *cylindracea* (see Table 2). The strain of *Ulva fasciata* discovered in the Northwestern Mediterranean (Thau Lagoon) is probably a new introduction

Table 3. Biogeographical affinity, in their native area, of the seaweeds introduced into the Mediterranean. Tropical = annual SST minimum >20°C. Temperate = annual SST minimum between 10°C and 20°C. Cold = annual SST minimum <10°C. See Lûning (1990) for definitions and SST maps.

		Biogeographical affinity of introduced species		
Period	**Number of introduced species**	**North and South cold**	**North and South temperate**	**Tropical**
1800–1940	21	4.3 (20%)	7.7 (37%)	9.0 (43%)
1941–1980	39	7.7 (20%)	14.0 (36%)	17.3 (44%)
1981–2008	46	16.2 (35%)	17.9 (39%)	11.9 (26%)

from Japan (unpublished data). Finally, the very localised new area of *Lophocladia lallemandii* (Balearic Islands, Spain), together with its proliferation, could also be indicative of a new introduction event (strain or yet unidentified taxon). (iv) The shrinking of the area of a cold-affinity species: Genetic processes such as inbreeding depression can account for this, in addition to warming. (v) The demonstration that introduced species of tropical origin are more invasive (more ‘aggressive’) that cold-affinity species: As pointed out by Perez (2008), this could prove to be correct for Prokaryota. As far as seaweeds are concerned, there is no indication that species of cold-water origin (such as *Sargassum muticum* and *Undaria pinnatifida*), e.g., in the Nortwestern Mediterranean Thau Lagoon, are less invasive than species of tropical origin (such as *Stypopodium schimperi*) in the warmer Eastern Mediterranean Sea.

In fact, it may simply be too early to detect a qualitative or a quantitative impact of warming on seaweed introductions, unless it is indeed an insoluble problem, or even a false problem.

5. General Discussion and Conclusion

It is difficult to give a definite answer to the question we asked (‘Is global warming involved in the success of seaweed introductions?’). Several distortions may affect the data set we used. (i) Study taxa and study areas largely depend upon the phycologists and their location. (ii) Large introduced species, belonging to taxa whose delineation is not controversial, are easier to detect than tiny species whose taxonomy is confused and accessible to very few specialists. (iii) Cryptogenic introductions are by definition unknown. Taking them into consideration, where it is possible, might conspicuously modify the baseline of our data set, i.e., the panel of anciently introduced species. (iv) Cryptic introductions are not taken into account, though progress in taxonomy will progressively make this possible. (v) The native area (and biogeographical province) of a species is not always accurately known. Either it is naturally present in unknown regions and the native area is underestimated, or it constitutes a cryptogenic introduction in part of its current area, and the native area is therefore overestimated.

Even taking into account these caveats, our data do not support the assumption that climate warming enhances biological invasions in the Mediterranean, at least in the case of the seaweeds. (i) The increase over time in the number of introduced species simply reflects the development of the vectors. In the early and mid-twentieth century, the Red Sea was the main donor region (Fig. 2). Subsequently, the relative strength of this vector declined. It can be hypothesised that most of the species from the Northern Red Sea, suited to survival in Mediterranean habitats and under their present conditions, have already taken the Suez Canal. In the 1970s, oyster culture took over from the Suez Canal as the main vector (Fig. 2). Since the turn of the century, oyster culture seems to be losing ground: either because oyster importation from Northwestern Pacific is officially banned or because most of the Japanese species that were able to thrive in the Mediterranean have been already introduced. In the absence of a new leading vector, the rate of introductions seems to be slowing down (Fig. 1; see also Galil et al., 2007, for Metazoa). Is this a durable trend or just a provisional one, i.e., waiting for the occurrence of the next prevailing vector? (ii) Since the 1980s, i.e., since the undisputable warming of Mediterranean surface water, not only has the relative percentage of new introduced species of tropical origin not increased, but also it has conspicuously declined (Table 3). The reason is that what matters first is the vector (see above). (iii) The alleged 'aggressiveness' of tropical introduced species, such as *Caulerpa taxifolia* and *C. racemosa* var. *cylindracea*, is due to the fact that they are seen as of tropical origin, when they are actually native to temperate seas. Their success in the Mediterranean, a temperate sea, is therefore in no way unexpected. (iv) The warming can advantage thermophilic introduced species. However, at the same time, it can disadvantage cold water species. The overall numbers of new introduced species and the overall dominance of introduced species might therefore be unchanged.

It is interesting to note that the simulation of the effects of climate warming and biological invasions (from 1900 to 2050) on the Mediterranean continental vegetation led to the conclusion that the driving force was the introduced species, whereas warming alone or in combination with introduced species was likely to be negligible in many of the simulated ecosystems (Gritti et al., 2006).

The link between climate warming and biological invasions is therefore poorly supported by the Mediterranean seaweeds. From a quantitative point of view, there are no grounds to believe that warming is responsible for the increase in the number of introduced species, or that species of tropical origin are more 'aggressive' than those of cold-water region origin. From a qualitative point of view (i.e., which species?) together with the spread and dominance of these species, the authors who claim that warming enhances the introduction, spreading and dominance of tropical species, are simply putting Descartes before the horse: if warming becomes more pronounced, which is unfortunately highly probable, there is no doubt that they will end up being proved right.

As far as the politicians, decision-makers and civil servants are concerned, their belief that the current increase in the number of introduced species results from global warming is not supported by the available data. There is no reason for this to change in the near future, and there is therefore no excuse for not implementing the international agreements for limiting and controlling biological invasions.

6. References

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