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REPORT

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Turbinaria ornata invasion in the Tuamotu Archipelago, French Polynesia: ocean drift connectivity

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Abstract This paper focuses on the invasion by *Turbinaria ornata* (a brown algae) in the Tuamotu archipelago, French Polynesia [(5–35°S)/(200–230°E)]. Prior to 1980, this alga existed only in the Society and Austral archipelagoes. Between 1985 and 1990, it began to appear in the southern and northern parts of the Tuamotu archipelago. Genetic analyses have been shown not to be appropriate in determining the origin of this algae population. This study investigated the possible ocean drift of floating aggregates of algae. Ocean currents were calculated from satellite data from 1993 to 2001. Their spatial variations as well as their seasonal and interannual variations are described along with calculated drift trajectories. While it was found that mean currents cannot directly transport algae from the Society and Austral archipelagoes to the Tuamotu, the large interannual changes during the El Niño-Southern Oscillation phenomenon produce current reversals that are strong enough to create a transport pathway in a short enough time to allow their survival.

Keywords Drift connectivity · Turbinaria ornata · Surface currents · French Polynesia

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Introduction

The presence of the brown algae *Turbinaria ornata* is noteworthy on the reefs in Tahiti and other high islands of French Polynesia (Fig. 1). *T. ornata* is one of the most conspicuous of the established macroalgae in terms of widespread distribution and high population density according to Stiger and Payri (1999a, b). Before the 1980s, this species was only observed in low density in the Society Islands (Payri and Naim 1982), and in the Austral Islands, except the Island of Rapa. After the strong 1983 El Niño event, the *T. ornata* population density increased particularly in the Society archipelago (Payri 1987). Subsequently, algal rafts begin to form and become abundant. In 1985, the algae started to appear in the north Tuamotu (Makatea: Montaggioni et al. 1985; Mataiva: Delesalle 1985; Rangiroa: Stiger and Payri 1999a, b; Payri et al. 2001). In 1990, the species was observed on the Moruroa reefs in the southern Tuamotu (Stiger and Payri 1999a, 2005). Meanwhile, the population biomass strongly increased on the reefs of the Society Islands, especially in Tahiti and Moorea (Payri 1987). However, the latest molecular analyses carried out on samples from different islands including Tuamotu atolls were inconclusive as regards to the origin of the samples (A. Rohfrisch, personal communication).

Several hypotheses for the observed spread have been examined. Stiger and Payri (1999a, b) showed that the dispersal distance of the zygote is limited to one meter from the parental thallii, precluding colonization between islands separated by several thousand kilometers. Long distance dispersal by ballast waters and ship biofouling are also unlikely because the species cannot survive in ballast waters, and ship inspections showed no presence of thallii fragments on hull or ballasts (Stiger and Payri 1999a, b). The appearance in the last two decades of large rafts of drifting algae in the open ocean suggests that an inter-island transport may have caused the spreading. Because drifting thallii rafts have a large biomass (Zubia 2003) and the thallii fertility lasts

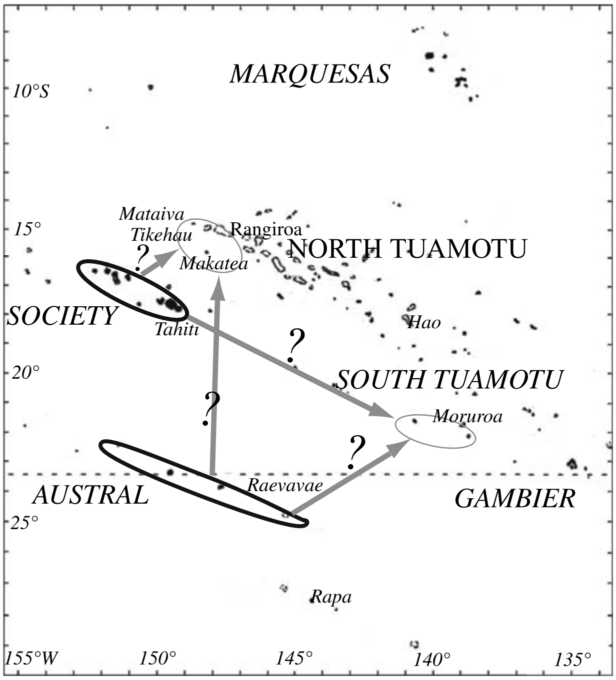

Fig. 1 Initial presence (*bold line*) and appearance areas (*thin line*) of *Turbinaria ornata* during 1980–2005 in French Polynesia. Archipelago names are in *capital letters* and island names are in *lower case*

3–4 months after they leave the reef, there is a possibility that thallii survive while drifting in the open ocean as large rafts, and go on to populate other islands. On such spatial scales, little is known about macroalgal dispersal by currents. Most of the studies dedicated to marine population dispersal based on current modeling mainly concern fish, crustacean and coral larvae (Cowen et al. 2000).

The purpose of the present study was to investigate this hypothesis for the colonization of the Tuamotu archipelago by *T. ornata* from the Society and Austral archipelagos.

Ocean currents in French Polynesia are poorly known, essentially because of the lack of data in the area. The few existing studies are based on scattered hydrographic data. The first substantial work on circulation in French Polynesia was derived from the Hawaii to Tahiti Shuttle Experiment (Wyrtki and Kilonsky 1984), which produced vertical conductivity-temperature-depth (CTD, providing temperature and salinity over the water column) profiles. From these, zonal geostrophic currents and transports were computed along the longitude 150°W, from Tahiti to the equator. Similar work was done using data from the "MARARA" cruises that were repeated twice yearly from 1986 to 1989, from Tahiti to Rapa, Tahiti to the Marquesas and the Marquesas to Moruroa (Boulanger et al. 1993; Rougerie and Rancher 1994; Rancher and Rougerie 1995). The southernmost part of French Polynesia has been studied using 12 surface drifters launched from Moruroa and Fangataufa atolls (Boulanger et al. 1993). More studies using other types of hydrographic data such as expendable bathy thermographs (XBT, which provide temperature over the top 400–800 m of the water column along ship tracks) have been done at the South Pacific scale including the French Polynesia region but without focusing on it (Kessler and Taft 1987; Lagerloef et al. 1999; McCarthy et al. 2000; Delcroix et al. 2005). The aforementioned studies identify two main features in the French Polynesian region: the westward flowing South Equatorial Current (SEC) between 0°S and 20°S, with stronger velocities during winter, and the eastward flowing South Pacific Current (SPC) of 20°S.

Because ocean currents display large spatial and temporal variations, hydrographic data alone are not appropriate to evaluate the Lagrangian displacements of drifting objects. Satellite sea surface height and wind data were used, therefore, to calculate instantaneous ocean currents at the sea surface and integrate those currents using a Lagrangian model to calculate the drift of floating rafts. This drift model was validated by comparison between drifting buoys from the World Ocean Circulation Experiment program and their simulated trajectories.

Several drifting scenarios were analyzed from different seasonal and interannual climate states. The observed migration of the algae is not explained by seasonal variations but may be associated with the oceanic currents during El Niño.

Materials and methods

Surface oceanic currents were calculated from sea surface height (SSH) and sea surface wind satellite data products from January 1993 to January 2001. Combined SSH data from the Topex/Poseidon and ERS1 and 2 satellites are available on a 1/3 grid every 7 days (Fu et al. 1994; Stammer and Wunsch 1994) and wind data from the ERS1 and 2 satellites are available on a 1 grid every 7 days (Ducet and LeTraon 2001). In the open ocean, surface currents are well approximated by the sum of the wind-driven currents, under the influence of direct friction forces, and the geostrophic currents, resulting from an equilibrium between the pressure and Coriolis forces. The method follows closely that of Lagerloef et al. (1999). Pressure forces are calculated from the absolute SSH. Because of a large uncertainty in the geoid, SSH from satellites are accurate only as an anomaly with respect to their long-term average. The long-term average was obtained from the Levitus (1982, http://www.nodc.noaa.gov/OC5/dyn.html) mean annual climatological dynamic height referred to 1,000 m depth. The surface geostrophic currents were obtained from this absolute dynamic height (Lagerloef et al. 1999). Geostrophy was established from the standard geostrophic balance. Because the Coriolis parameter vanishes at the equator, there is a transition occurring at about 3°S and the so-called β-plane formulation (where β is the rate of change of f with latitude) was used (Lagerloef et al. 1999).

Surface currents due to Ekman drift were calculated from the wind field as in Pond and Pickard (1983) and Chen et al. (1999). ERS1 and 2 wind products provided by PODAAC were linearly interpolated, temporally and spatially, to the SSH grid. The wind stress coefficient $\tau = \rho_a C_d W^2$ (ρ_a is the air density, C_d the drag coefficient and W the wind speed) allows calculation of $V_o = (\tau\pi\sqrt{2})/(D_e\ \rho\cdot|f|)$ (ρ is the water density, D_e the Ekman depth taken equal as 32 m (Lagerloef et al. 1999), and f the Coriolis parameter), the magnitude of the total Ekman surface current, and then by a projection to obtain meridian and zonal vector components. Various models of the flow within the Ekman layer have been used. For instance Madsen (1977) used a vertical viscosity that is linearly depth dependant and obtains deflection angles ranging from 10° at the surface to about 60° at 16 m for a 32-m Ekman depth. Given the uncertainties in the angle definition, the deflection angle at 45° to the left of the wind field was chosen, as in Kubota (1994).

The model neglects vertical diffusion, local acceleration, wind-borne drag and Stokes drift. According to Bonjean and Lagerloof (2002) and Lagerloef et al. (1999), vertical diffusion and local acceleration have little impact on surface velocities out of the equatorial band. The direct wind drag on the algae rafts is also probably very small as algae drift just underneath the surface. The long swell poses a real Stokes drift if it is consistently from one direction. However, French Polynesia is dominated by 2–4 m s^{-1} easterly winds (Laurent et al. 2004) that lead to a less than 5 cm s^{-1} westward wave drift. Consequently, even if it could have a strong impact in fast developing stormy conditions (Andréfouët et al. 2002; Perrie et al. 2003; Weber 2003; Lewis and Belcher 2004), this drift contribution is smaller than the currents affecting the region and can justifiably be dropped as already shown by Kubota (1994) and Kubota et al. (2005).

The sum of geostrophic and Ekman currents determines the surface currents from 1993 to 2001 with a 7 day timestep.

The trajectories of the algal rafts detached from the Society and Austral reefs were determined using Lagrangian equations as has been done on large scales in the North Pacific (Wakata and Sugimori 1990; Kubota 1994; Kubota et al. 2005). At any time, the raft positions are calculated in spherical coordinates by

$$\frac{d\theta}{dt} = \frac{1}{a\cos(\lambda)}U(\lambda,\theta,t) \qquad \frac{d\lambda}{dt} = \frac{1}{a}V(\lambda,\theta,t),$$

where a is the Earth radius, and longitude θ and latitude λ are the unknown coordinates. U and V are, respectively, the zonal and meridional surface current components. The equations are solved by a Runge-Kutta method as in Wakata and Sugimori (1990). The rafts are assumed to be passive (i.e., non-swimming) which is the case for *T. ornata* once they detach from the reef. Direct wind and Stokes drift were ignored, which is a reasonable approximation in the case of *T. ornata* rafts (see Discussion section).

The drift time was fixed at 4 months in accordance with the observed fertility of the thallii once they are torn off the reefs. Algal rafts were released monthly in the model from January 1993 to September 2000, from the Society and the Austral Islands, except Rapa.

Results

French Polynesia is dominated by two seasons: the wet season (November–April) and the dry season (May–October). The estimate of the surface currents shows that during the wet season (Fig. 2b) the southwestward SEC flows across the Marquesas archipelago [(6°S–12°S)] with velocities reaching 50 cm s^{-1}. Surface current velocities weaken towards high latitudes. Around the Tuamotu and Society Islands, the SEC decreases to 15 cm s^{-1}, and 5–10 cm s^{-1} further south (Austral and Gambier). For latitudes higher than 20°S, eddy-like structures are observed between 24°S and 30°S, noticeably in the transition zone between the SEC and the eastward SPC (Stramma et al. 1995). In the northwest part, from 8°S to 12°S, an eastward component indicates the eastern extremity of the South Equatorial Counter Current (SECC). During the dry season (Fig. 2a), the SEC intensifies everywhere with speeds reaching 60 cm s^{-1} in the north-east and around the Marquesas Islands. From 5°S to 20°S, the flow has a stronger westward component than during the wet season (a 20° clockwise rotation). The SECC vanishes during the dry season. At 20°S, the SEC joins the meandering convergence zone, which occupies a thinner latitude band than during the wet season. The SPC has moved to the north and has larger velocities (5–10 cm s^{-1}).

The interannual El Niño-Southern Oscillation (ENSO) has a strong influence on the French Polynesian climate (Laurent et al. 2004). ENSO affects the atmospheric and oceanic circulation and their seasonal variations described above. The El Niño 1997/1998 event was the most intense ever observed (Doumenge 1999; Picaut and Busalacchi 2001).

The impact of El Niño 1997/1998 is shown in Fig. 3, which can be compared to Fig. 2. Early after the onset of the El Niño (July 1997, Fig. 3a), no changes are observed in the north part of the region, currents are directed south-westward with speeds up to 50 cm s^{-1}. From 5°S to 15°S and west of 144°W, the meridional component is weakened. The southwestward current is about 20–30 cm s^{-1}. South of 18°S, the SEC strengthens (10–30 cm s^{-1}) and the eddy field becomes more intense. In February 1998 (Fig. 3b), the classical flow pattern of the SEC is dislocated although still visible in the northeast part of the figure. The SECC is more intense in

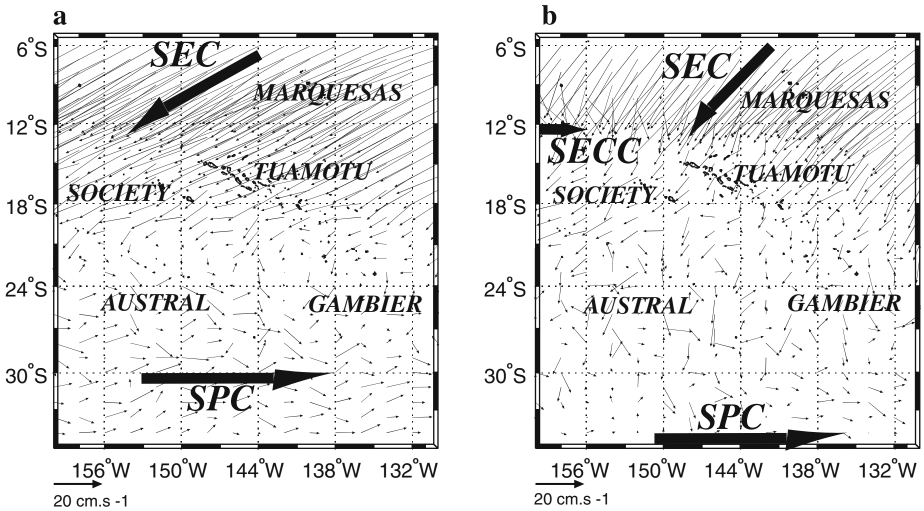

Fig. 2 Mean surface currents in French Polynesia during: **a** the dry season (July) and **b** the wet season (December), monthly mean. Archipelago names are in bold. *Arrows* show the surface currents (*SEC* South Equatorial Current, *SECC* South Equatorial Counter Current, *SPC* South Pacific Current)

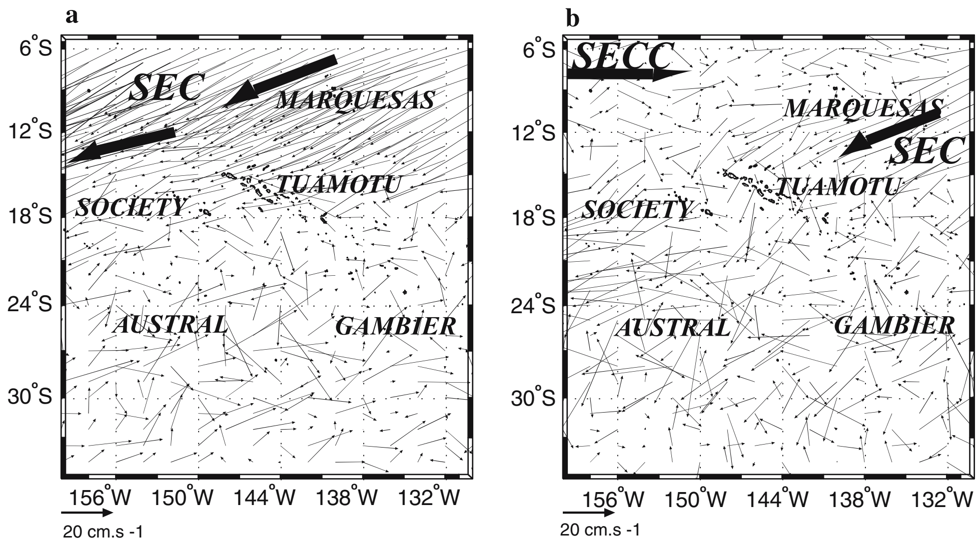

Fig. 3 Mean surface currents in French Polynesia during El Niño in: **a** July 1997 and **b** February 1998. Archipelago names are in *bold*. *Arrows* show the surface currents (*SEC* South Equatorial Current, *SECC* South Equatorial Counter Current, *SPC* South Pacific Current)

the northern region [(5°–12°S)-west of 135°W] with eastward flow and velocities reaching 15 cm s^{-1}. From 18° to 24°S, west of 150°W, the southwestward flow is intense with velocities between 40 and 50 cm s^{-1}. East of 150°W, eddies are ubiquitous with currents reaching a value of 30 cm s^{-1}. South of 30°S, weak flow is observed. During La Niña in the 1998 winter (Fig. 4a) currents intensify everywhere. They reach 60–80 cm s^{-1} in the north and 20–30 cm s^{-1} in the swirling central zone. The southwestward SEC extends far south, down to 22°S. Southwards, currents in the swirling zone are stronger (20–30 cm s^{-1}). The SPC has shifted south from 25°–26°S to 32°S. In February 1999 (Fig. 4b), compared to a normal period, the southwestward SEC weakens south of 10°S. Currents are stronger and eddy-like south of 18°S (30–40 cm s^{-1} down to 30°S and 10–20 cm s^{-1} southwards). The SPC cannot be identified because of the turbulent flow.

Having determined the surface currents, the seasonal and interannual variability in seaweed raft trajectories were described. The raft trajectories were modeled as imaginary floats released at the Society and Austral archipelagoes every month over the 8 years of data and for a 4-month drift.

Presented in Fig. 5 are the results for particles released on March 1995, representative of average climate conditions (i.e., non-El Niño nor La Niña). Floats originating from the Society and Austral Islands follow seasonal variations of the surface currents. During the wet season (Fig. 5a), floats from the Society Islands drift southward or southwestward until they exit the SEC influence. Then, they turn eastward as they reach the SPC. From the Austral Islands, floats cross the mid latitude eddy area and follow the eastward SPC. During the dry season (Fig. 5b), from the Society archipelago, the floats flow mainly west-southwestward. Most are ejected from the French Polynesian Economic Exclusive Zone and do not show up on the map. Austral Island floats remain more concentrated within the archipelago west of 144°W. For both seasons, particles never

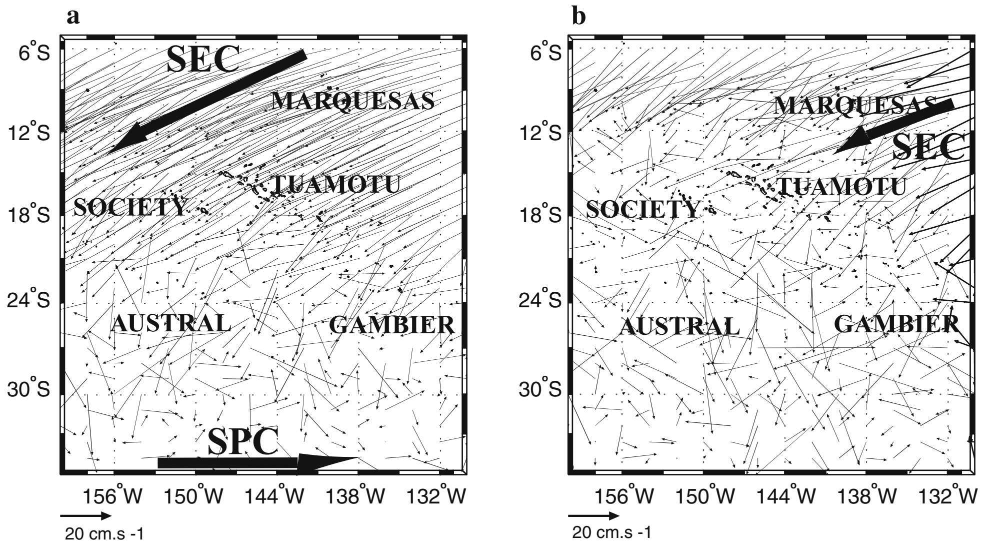

Fig. 4 Mean surface currents in French Polynesia during La Niña in: **a** July 1998, and **b** February 1999. Archipelago names are in *bold*. *Arrows* show the surface currents (*SEC* South Equatorial Current, *SECC* South Equatorial Counter Current, *SPC* South Pacific Current)

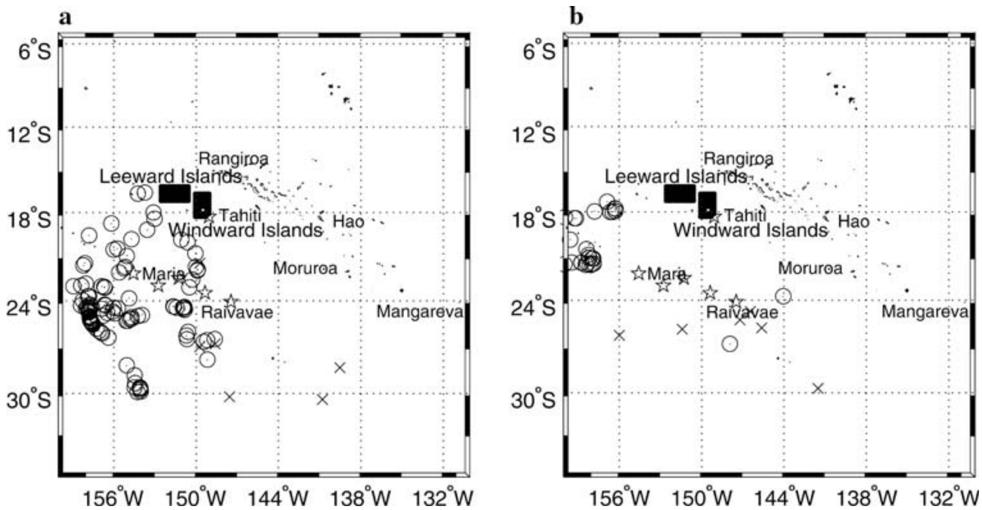

Fig. 5 Float positions, after 4 months during: **a** the wet season (March 1995) and **b** the dry season (August 1995), from Society and Austral archipelagoes. The initial drifter location for the five Austral Islands except Rapa, are represented by *stars* and the final position by *crosses*. Because drifters from the Society Islands are more numerous their initial positions are represented by the *black rectangles* (sampled every 0.2° in latitude and longitude) which represent the "Leeward Islands" (*horizontal rectangle*) and the "Windward Islands" (*vertical rectangle*) and their final positions by *circles*

significantly approach the Tuamotu archipelago. No raft reaches the Tuamotu or Gambier region. Thus the observed invasion of *T. ornata* in 1985 was not be explained by a drift such as the modeled 1995 trajectories from the Society and Austral Islands. Other release dates that are typical of the seasonal circulation lead to the same conclusions. The effects of interannual variations have to be considered.

T. ornata was observed in the Tuamotu 1 year after the strong 1983/1984 El Niño. It is not possible to estimate the circulation during this period, as satellite data were not available. However, satellite data were available during other El Niño events as in 1997/1998, a strong event similar to 1983/1984 and 1993/1994. The data for 1997/1998 and also 1993/1994 were used, therefore, to test the hypothesis of rafts reaching the Tuamotu and Gambier during an El Niño event.

During both El Niño and La Niña, floats from both Society and Austral Islands reach Southern Tuamotu at Moruroa and nearby islands (January and February 1994, December 1998–February 1999) (Fig. 6) or significantly approach them (December 1993; August 1997; December 1998; January, February, and June 1999). In this last case, simulations show that floats could reach the Southern Tuamotu after a 1 or 2-month drift. The Society and Austral Islands may therefore be linked with the Tuamotus during El Niño or La Niña, which is consistent with the hypothesis that the strong 1983/1984 El Niño may have allowed algae to populate the Tuamotu archipelago.

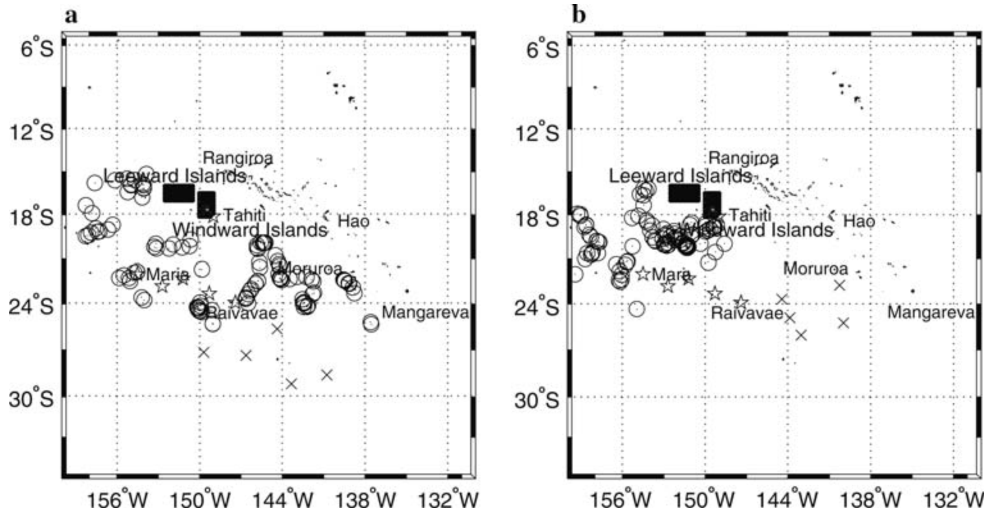

Fig. 6 Float positions, after 4 months during: **a** February 1994 and **b** June 1999, from Society and Austral archipelagoes. The initial drifter location for the five Austral Islands except Rapa, are represented by *stars* and the final position by *crosses*. Because drifters from the Society Islands are more numerous their initial positions are represented by the *black rectangles* (sampled every 0.2° in latitude and longitude) which represent the ''Leeward Islands'' (*horizontal rectangle*) and the ''Windward Islands'' (*vertical rectangle*) and their final positions by *circles*

A complete analysis of the trajectories showed that some floats originating in the Society Islands during El Niño or La Niña move northward or northeastward before turning and flowing southwestward or westward along the SEC. This occurs in April and December 1993; January, February, and March 1994; January and May 1995; April and July 1997; and January 1998. Although those trajectories never reach Northern Tuamotu, they significantly approach them (Fig. 7). This result, which does not appear in the seasonal average circulation, suggests that episodic contacts might occur between the Society and Northern Tuamotu Islands.

Discussion

The estimate for the flow field is derived from unprecedented high resolution and high accuracy satellite data. Nevertheless, the model used to link the flow field with the data, and then to integrate float trajectories uses a number of necessary approximations. To quantify the model error, trajectories were calculated for 40 particles corresponding to real surface velocity program (SVP) Lagrangian drifters that were launched for the World Ocean Circulation Experiment (http://www.ewoce.org/data/index.html). Within this global experiment, some drifters were launched in the French Polynesian Exclusive Economic zone (EEZ) every year from 1993 to 1999. SVP drifters are satellite-tracked and drift 15 m below the surface for about a year. The model is constructed to give the trajectories of surface floats, and the comparison with the SVP drifters whose drogue is 15 m below the surface introduces an additional but small error because of the vertical shear and azimuth change near the surface related to the Ekman layer dynamics.

For the purpose of clarity, four SVP drifter trajectories are displayed (Fig. 8), along with their simulated trajectories. The SVP drifter which started in January 1996 in the northeastern part of the EEZ (Fig. 8, trajectory A) is located in the SEC (*white square* on right panel). The modeled trajectory is similar in the first part of the journey. The pathway is then influenced by small-scale currents due to the islands and seamounts around the Marquesas archipelago and the Tuamotu Islands. As a result the SVP drifter slows down and meanders. Those small-scale features are not well resolved in the satellite data, and the modeled trajectory goes straight through the archipelagos and arrives further south. The other three drifters are launched in the transition zone, as previously described, where eddy-like structures are observed (Fig. 2). To first order, the modeled trajectories are similar to the observed ones. For instance, drifter *D* (Fig. 8) released at 30°S goes westward before turning eastward along the SPC. The details in the meanders cannot be fully resolved by the model's limited spatial and temporal resolution. The Lagrangian model is therefore producing realistic trajectories on the large scales. This comparison highlights the southwestward main trend of the surface drift in the northern part of the region even if some drifters are delayed around the

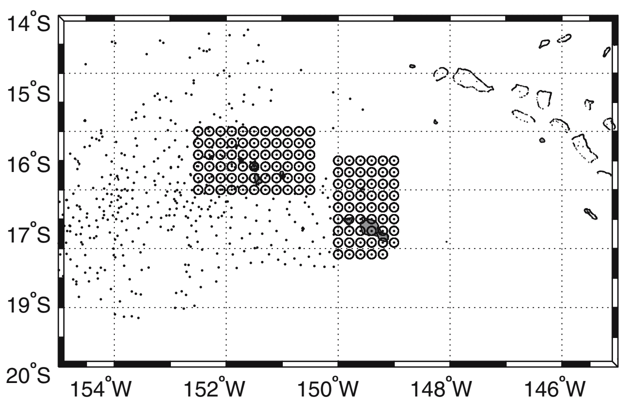

Fig. 7 Float positions with a start from Society archipelago in January 1998. The initial drifter location from the Society Islands are represented by a *circle with a point inside*. The positions at each time step are represented by a *point*

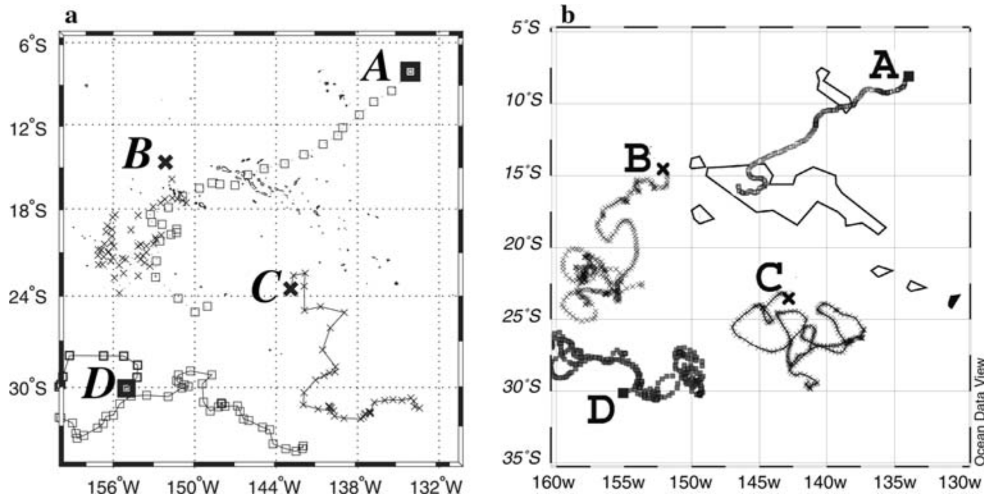

Fig. 8 Comparison between: **a** satellite and **b** WOCE drifters. The drifter release locations are marked by large symbols. The trajectory A is from 1 January to 24 December 1998 (*black squares with a continuous line*), B is from 1 January to 31 December 1993 (*stars with a dotted line*), C is from 1 January to 30 September 1999 (*black stars with a continue line*) and D is from 1 January to 11 July 1996 (*white squares*). On the left hand, the *black contours* represent the archipelagoes

Tuamotu archipelago. Trajectory errors also occur in the southern part of the EEZ where the flow is more turbulent. SVP drifters show that small, unresolved eddies can capture some floating rafts.

In conclusion, and given the limitations of the model inherent to the available data set and simplified dynamics (see the "model" section), *T. ornata* from Society and Austral archipelagoes can reach the Southern Tuamotu during the peaks of La Niña or El Niño events. This invasion had not been noticed before 1983, for at least two reasons: (1) an increasing anthropic pressure there was not enough biomass before 1983 to form significant rafts and (2) the El Niño 1983 was of unprecedented amplitude. Hazell and England (2003) used a numerical model to estimate the dispersion of a radioactive tracer away from Moruroa atoll and found an influence by seasonal and interannual variations similar to these results. They found that radionuclide tracers released at the surface were trapped inside the Polynesian EEZ during an El Niño year, in a similar way to the simulated drifters in the present study.

The colonization of the northern part of the Tuamotu is not explained by the modeled drifts, even though a tendency to drift from the Society Islands towards Rangiroa is observed during the peaks of El Niño. Considering the multitude of islands in the center of the Tuamotu archipelago, the possibility was investigated that *T. ornata* rafts could have drifted from Moruroa towards Northern Tuamotu during climate anomaly periods via the center of the archipelago. The number of scientifically unexplored islands and the probably low density of the algae could explain why they have not yet been noticed by biologists. Some simulations with initial positions at Moruroa show swirling trajectories mainly directed southwestward or southeastward. During El Niño peaks, northward turbulent trajectories allow rafts to reach the center of the Tuamotu archipelago, all the way to Hao [(18°S–140°W), figure not shown]. But even during the peaks of El Niño or La Niña, no trajectory linked Hao to Rangiroa. Those supplementary experiments cannot establish the missing link. However, unresolved small scales, Ekman drift uncertainty, occasional storms and the structural differences between the 1983 and 1997 El Niño all may lead to inter-island raft propagation within an archipelago.

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