

Satellite remote sensing for an ecosystem approach to fisheries management

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Satellite remote sensing (SRS) of the marine environment has become instrumental in ecology for environmental monitoring and impact assessment, and it is a promising tool for conservation issues. In the context of an ecosystem approach to fisheries management (EAFM), global, daily, systematic, high-resolution images obtained from satellites provide a good data source for incorporating habitat considerations into marine fish population dynamics. An overview of the most common SRS datasets available to fishery scientists and state-of-the-art data-processing methods is presented, focusing on recently developed techniques for detecting mesoscale features such as eddies, fronts, filaments, and river plumes of major importance in productivity enhancement and associated fish aggregation. A comprehensive review of remotely sensed data applications in fisheries over the past three decades for investigating the relationships between oceanographic conditions and marine resources is provided, emphasizing how synoptic and information-rich SRS data have become instrumental in ecological analyses at community and ecosystem scales. Finally, SRS data, in conjunction with automated *in situ* data-acquisition systems, can provide the scientific community with a major source of information for ecosystem modelling, a key tool for implementing an EAFM.

Keywords: ecosystem approach, fisheries, mesoscale, satellite, tracking.

Introduction

Since the birth of the space age in the late 1950s, developments in platform and sensor technology, data storage and transfer, and the increasing demand for satellite data products have combined to support the rapid expansion of satellite remote sensing (SRS) civil applications: meteorology, aviation, positioning, and communication. In addition, remotely sensed satellite data have proven to be valuable tools in different applied fields, such as agriculture, land use, and hydrology. Satellites have now become instrumental in ecology for environmental monitoring, e.g. biogeochemistry and physical oceanography, and are promising tools for conservation issues (Turner *et al.*, 2003; Mumby *et al.*, 2004).

Although conventional fisheries management has focused mainly on single-species approaches in recent decades, the ecosystem approach to fisheries management (EAFM), promoted by the Food and Agriculture Organization of the United Nations (FAO), recognizes the importance of maintaining the complexity, structure, and function of marine ecosystems and of ensuring the sustainability of the fisheries and human communities they support (Garcia *et al.*, 2003). In particular, a major objective of the

EAFM is to expand the consideration of fish population dynamics to their marine habitats, to move progressively towards an end-to-end ecosystem approach (Cury *et al.*, 2008). The EAFM aims to improve understanding of the determinants of changes in the abundance and spatial distribution of exploited fish stocks, to disentangle fishing effects from environmental forcing, and eventually to implement more-effective management systems (Botsford *et al.*, 1997; Garcia *et al.*, 2003; Cury *et al.*, 2008).

In this context, the availability of global, daily, systematic, high-resolution images obtained from satellites has been a major data source for elucidating the relationships between exploited marine organisms and their habitat (Polovina and Howell, 2005; Dulvy *et al.*, 2009). Some past reviews addressed the use of SRS of the marine environment, but focused mainly on case studies of applied fishery oceanography where short-term forecasting systems were developed in support of fishing activities (Tomczak, 1977; Yamanaka, 1988; Le Gall, 1989). Butler *et al.* (1988) provided a comprehensive report on the use of remote sensing in marine fisheries during the 1980s, describing satellite platforms, sensor systems, and digital image-processing techniques and providing a synthesis of more than 20 case studies

based on airborne and spacecraft remote-sensing data. Since then, considerable progress has been made in SRS data acquisition and processing, and substantial numbers of new high-resolution datasets have become fully accessible for analyses in addition to *in situ* survey and fishery data. During the past decade alone, the application of satellite datasets has been extended progressively to encompass both data-driven and ecosystem-modelling approaches in marine ecology. The objectives of this paper are to: (i) provide an overview of current satellite platforms and sensors, dataset availability/accessibility, and image-processing techniques for studying mesoscale features of particular relevance to EAFM (Cury et al., 2008); (ii) conduct a comprehensive review of satellite remotely sensed data applications by investigating the relationships between oceanographic conditions and marine resources, including the geolocation of marine species and characterization of preferred habitats along migration routes using satellite tags; (iii) demonstrate how synoptic and information-rich SRS data have become instrumental in ecological analyses at community and ecosystem scales; and (iv) discuss the assumptions, limits, and caveats associated with the use of SRS data, and challenges for the near future.

SRS data acquisition and products from global to mesoscale

Sensors, datasets, and processing

Many satellites and remote sensors provide data on oceanographic parameters that are now available to the scientific community as standard products. The most common time-series datasets and the main principles of image-processing algorithms and data formats are presented below.

In the context of SRS, a sensor is an electronic device that detects emitted or reflected electromagnetic radiation and converts it to a physical value that can be recorded and processed. In terms of the type of energy source, radiometers can be divided into passive sensors, which detect the reflected or emitted electromagnetic radiation from natural sources [temperature, ocean colour (OC)], and active sensors (radars, scatterometers, and lidars), which detect reflected responses from irradiated objects (Butler et al., 1988). Sensors can be classified into four types according to the spectral regions of solar radiation: (i) visible and reflective (or “near”) infrared (domain of ocean-colour radiometry), (ii) mid-infrared, (iii) thermal infrared, and (iv) microwave (Martin, 2004). Practically, the wavelength intervals or spectral bands are chosen according to their relatively low atmospheric absorption, which is spectrally highly variable. For example, the main atmospheric windows for the measurement of sea surface temperature (SST) in the mid- and far-infrared part of the solar spectra are ~ 3.7 and $11\text{--}12\ \mu\text{m}$, respectively.

SRS imaging systems are generally characterized according to their spatial, temporal, and spectral resolutions (Campbell, 2007;

Table 1). The spatial resolution specifies the nominal pixel size of the satellite image, and the temporal resolution specifies the revisiting frequency of observation for a specific location. A sensor’s spectral resolution specifies the number, width, and position in the electromagnetic spectrum of spectral bands where it can collect reflected radiance. An exhaustive list of the available SRS datasets is beyond the scope of this review, so we present only the most common and useful relevant parameters: SST, sea surface salinity, windspeed, sea surface height (SSH), chlorophyll *a* (Chl *a*), and Chl *a*-derived primary production (Table 2).

SRS data products are classified according to the processing level, from raw to end-user data (Table 3). Raw data constitute the first level, referred to as level 0, which contains all the orbital telemetry information, calibration coefficients, and various ancillary data, as well as the raw data from the sensors, often in a complex multiplexed form. These data cannot be processed easily outside specialized centres. Level 1 data contain the same data as level 0, but are reorganized by channel and are in various sublevels, from raw measurements to geophysical units (top of atmosphere irradiance and brightness temperature). Data are in the orbit form, i.e. satellite coordinates. Level 2 data are still in the orbit form, but include geolocation and atmospheric corrections. For many scientific users, this is the first exploitable data level. Level 2 data contain the end-user geophysical parameters (i.e. normalized water-leaving radiance or reflectance, SST) and make use of meteorological information from ancillary sources. In addition, this level contains a number of variables of scientific interest that can be retrieved from various sensors on board different satellites and computed with specific algorithms. For SST retrieval, Figure 1 summarizes the main processing steps applied to the signal measured by the sensor to obtain first a measured radiance (expressed in $\text{W m}^{-2} \text{sr}^{-1} \mu\text{m}^{-1}$), then the top-of-atmosphere “brightness temperature” (the theoretical temperature if atmosphere and ocean were black bodies, i.e. absorbing and re-emitting all the energy they receive), and finally a valid SST measurement. This last and most critical step consists of inverting a radiative transfer model that theoretically describes the alteration of the original signal through the atmosphere before it reaches the sensor. These models are complex; they assume a precise knowledge of the emissivity of the atmosphere and ocean, which is lower than from a black body. Practically, this step is generally done with empirical algorithms that take advantage of the differences in the atmospheric alteration of the signal within two (or more) distinct wavelengths. SST is computed as a sum of linear combinations of the brightness temperature measured in these different wavelengths. The coefficients of the relationship are determined by a minimization process using match-up *in situ* measurements from buoys. Similar data processing is applied to OC measurements, whose most important optical component is the upward water-leaving radiance just above the sea surface (L_w), a value that depends on the absorption and backscattering properties

Table 1. Main ranges of spatial, temporal, and spectral resolutions used in the terrestrial and global environment, including marine and atmospheric domains.

Resolution	Environment	Low resolution	Medium resolution	High resolution
Spatial	Terrestrial	30–1000 m	4–30 m	0.4–4 m
	Marine	10–50 km	2–10 km	≤ 1 km
Temporal	Terrestrial	> 16 d	4–16 d	1–3 d
	Marine	> 5 d	1–5 d	≤ 1 d
Spectral	–	1 channel (e.g. panchromatic)	3–10 channels	≥ 10 channels (hyperspectral)

Table 2. Main sensors and datasets of interest for oceanographers and fishery scientists, with all products level 3 gridded, except where explicitly mentioned otherwise.

Parameter	Institution	Sensor	Platform	Temporal resolution	Spatial resolution	Period
SST	NASA OBPG	MODIS	EOS AQUA	d, week, month, Clim.	9 km, 4.5 km	July 2002→
SST	NASA PO-DAAC	Pathfinder V5	NOAA AVHRR	d, week, month, season, Clim.	4.5 km	January 1985 → December 2005
SST	NASA PO-DAAC	Pathfinder V4, V5	NOAA AVHRR	Week, month, Clim.	9 km	January 1985 → 2003/08
SST	OSI-SAF EUMETSAT	SEVIRI	MSG, GOES-east	3–12 h, hourly	1/10°, 1/20°	July 2004→
SST	OSI-SAF EUMETSAT	METOP	AVHRR	d, (2 d ⁻¹ : 00–12 h)	1/20°	July 2007→
SST	OSI-SAF EUMETSAT	METOP (Level 2)	AVHRR	d (2 d ⁻¹), 3-month granule orbit	1 km	November 2009→
SST	NASA REMSS	TRMM	TMI	d, 3-d, week, month, Clim.	1/4°	November 1997→
		AQUA	AMSR-E			August 2002→
SSS	ESA CNES	MIRAS (Level 1/2)	SMOS	10–30 d	50–200 km	January 2010→
Chl <i>a</i>	NASA OBPG	MODIS	EOS AQUA	d (1 d ⁻¹), 3-d, 8-d, month, Clim.	4 km	July 2002→
Chl <i>a</i>	NASA OBPG	SeaWiFS	SeaStar	8-d, month, Clim.	9 km	December 1997→
Chl <i>a</i>	NASA OBPG	MODIS (Level2)	EOS AQUA	d, 5 month orbit	250 m, 500 m, 1 km	July 2002 →
Chl <i>a</i>	ESA GLOBCOLOR	MERIS	ENVISAT	d, week, month	300 m, 1 km	March 2002→
Windspeed	IFREMER CERSAT	ERS	AMI	8-d, month, Clim.	1°	August 1991 → April 2002
wind direction		QuickScat	Seawind		1/2°	December 1999 → November 2009
Windspeed	NASA REMSS	QuickScat	Seawind	d, 3-d, week, month	1/2°	December 1999 → November 2009
wind direction						
Windspeed	NASA REMSS	SSM/I	DMSP series	d, 3-d, week, month	1/4°	July 1987→
		TMI	TRMM			December 1997→
		AMSR-E	EOS-AQUA			August 2002→
SSH	CLS AVISO	ERS-TOPEX-JASON	–	Week (delayed time)	1/3°	October 1992→
SLA				d, J ⁻¹ , J ⁻⁶ (real time)		
PP	NASA OBPG	SeaWiFS (Chl <i>a</i> , PAR, SST)	–	8-d, month	9, 18 km	October 1997 → December 2008
PP	NASA OBPG	MODIS (Chl <i>a</i> , PAR, SST)	–	8-d, month	9, 18 km	July 2002 → December 2007

Clim., climatology; SLA, sea level anomaly; SSH, sea surface height; SST, sea surface temperature; AMI, active microwave instrument; AMSR-E, advanced microwave scanning radiometer for the Earth Observing System; AVHRR, advanced very high resolution radiometer; AVISO, archiving, validation, and interpretation of satellite oceanographic data; CERSAT, Centre ERS d'Archivage et de Traitement; CLS, collecte localisation satellites; DMSP, Defense Meteorological Satellite Program; EOS, Earth Observing System; ENVISAT, ENVironmental SATellite; ERS, European remote sensing; ESA, European Space Agency; IFREMER, Institut Français de Recherche pour l'Exploitation de la MER; GOES, geostationary operational environmental satellite; HDF, hierarchical data format; MODIS, MODerate resolution Imaging Spectrometer; MSG, Meteosat second generation; NASA, National Aeronautics and Space Administration; NetCDF, network common data form; NOAA, National Oceanic and Atmospheric Administration; OBPG, Ocean Biology Processing Group; OSI-SAF, Ocean and Sea Ice Satellite Application Facility; PAR, photosynthetically active radiation; PO-DAAC, Physical Oceanography Distributed Active Archive Centre; QuickScat, quick scattermeter; REMSS, remote sensing system; SeaWiFS, Sea-viewing Wide Field-of-view Sensor; SEVIRI, spinning enhanced visible and infrared imager; SSM/I, special sensor microwave/imager; TMI, TRMM microwave imager; TOPEX, The Ocean Topography Experiment; TRMM, Tropical Rainfall Measuring Mission.

Table 3. Conceptual scheme of the data processing of the most common oceanic parameters, from the raw (level 0) data to geophysical variables (upper part) and post-processing of variables data to compute specialized level 4 parameters (lower part).

Level 0 parameter	→ Level 1 parameter	→ Level 2/3 (geophysical variable)
Brightness temperature for two or three infrared wavelengths	Calibration, inversion of Planck's law, cloud masking, atmospheric correction (split-window algorithm)	SST (°C)
Normalized water-leaving radiances at six wavelengths	Calibration, band combination, cloud masking	Chl <i>a</i> (mg m ⁻³)
Surface backscatter coefficient (σ)	Cox and Munk (1954) model ($\sigma = aWb$)	Windspeed and direction (if multidirectional measures)
SSH	Pseudogeoid (average signal) subtraction	SLA
Input geophysical variables	Processing scheme	→ Level 4 meta-variable
SST	Convolution (e.g. Sobel operator)	Local SST gradient (°C km ⁻¹)
SST	Determination of limits between water masses	Frontal positions
Chl <i>a</i> , photosynthetically available radiation (PAR), photosynthetic efficiency curve	Equation of water attenuation and photosynthetic efficiency relationship	Primary production (mg C m ⁻² d ⁻¹)
SLA	Application of baroclinic instability	Geostrophic currents

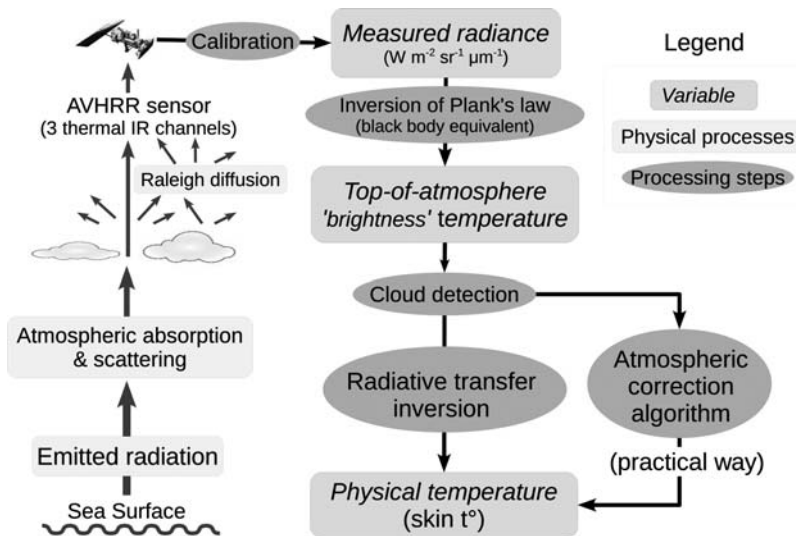


Figure 1. Typical processing steps of a thermal signal measured by a satellite remote-sensing sensor according to its physical transformations. The case of SST measured by the AVHRR sensor.

(referred to as inherent optical properties) of marine components (pure seawater, suspended or dissolved constituents). The concentration of Chl *a*, the dominant pigment in marine phytoplankton that makes the sea green, is computed from specific OC algorithms, usually from the remote-sensing reflectance (the sunlight reflected from below the sea surface, computed as the ratio of the normalized L_w to the solar irradiance in 3–5 wavelengths).

The data processing of a thermal signal for computing SST initially depends on the radiance measured by the sensors. Hence, different satellites and sensors will provide different spatial coverage and estimates of SST (Figure 2). For instance, the high observation frequency of the geostationary METEOSAT satellite (15 min) allows better declouding through data processing, whereas the microwave sensor TMI is unaffected by cloud cover (except for heavy rain) at the cost of lower resolution (25 km), lack of coastal data, and narrow swathes that result in observation gaps between 50°S and 50°N. The SST product combining data from several sensors is fully cloud-free (Figure 2), but

the blending process could make it less useful for describing mesoscale features and for climatological studies.

Level 3 data are the most widely distributed to the scientific community and are available from various archive sources. This level may contain a large number of parameters, including, for example, Chl *a* concentration from various algorithms, chlorophyll fluorescence efficiency, total suspended matter, and SST with quality levels. All data are gridded using a cartographic projection and often are averaged temporally and spatially. Level 4 includes higher-level composite products that require parameters and model applications not necessarily extracted from SRS (e.g. primary production, composite SST). To use the most relevant SRS product for scientific application, it must be emphasized that many uncertainties linked to the intrinsic nature of the physical models result in consequent uncertainties in the geophysical variables obtained, even more so for those derived through empirical algorithms. Table 3 gives an indication of the typical errors associated with the most common SRS geophysical parameters. For many

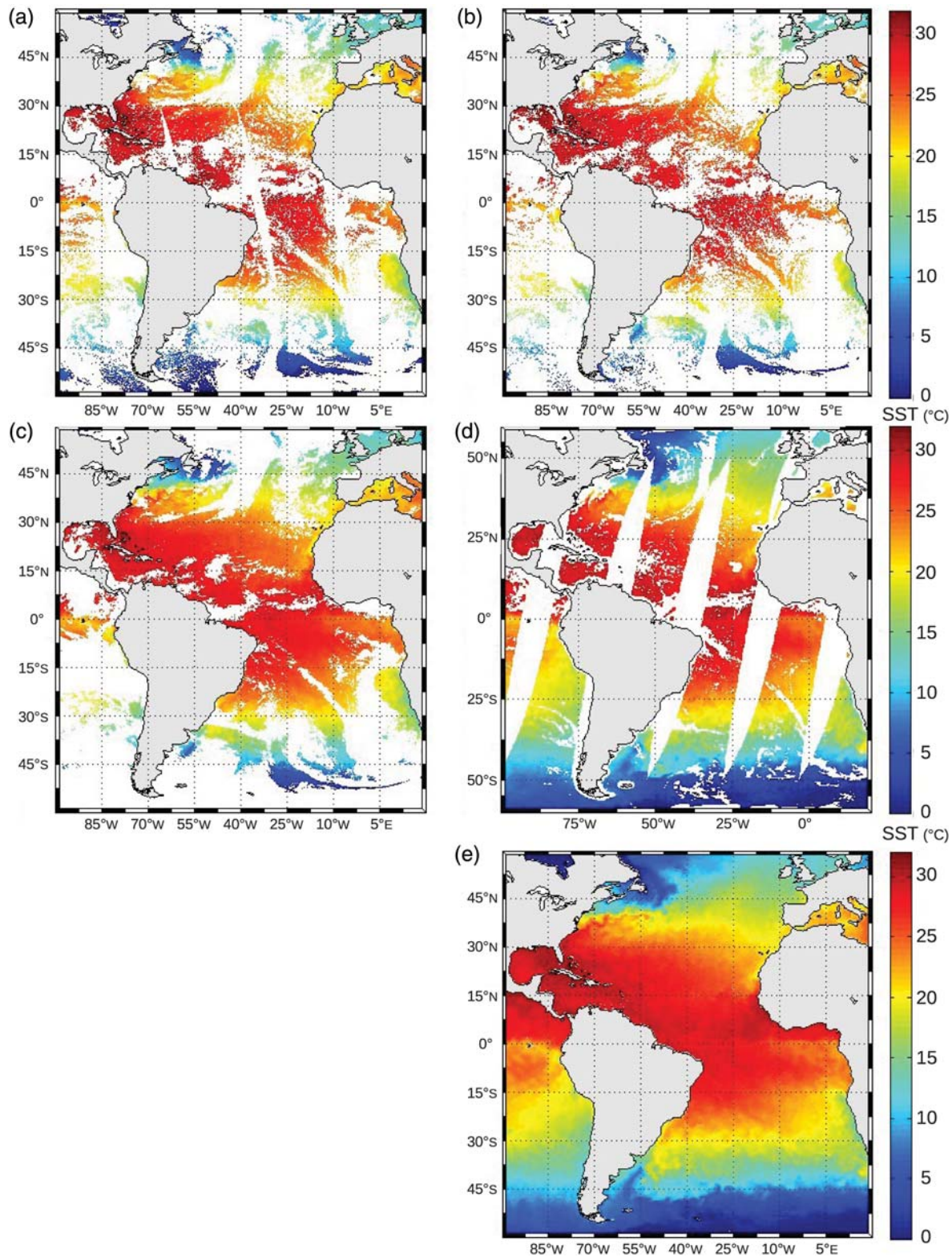


Figure 2. Example of daily SST products over the Atlantic Ocean on 18 June 2010 from three thermal-infrared sensors, (a) MODIS/AQUA, (b) AVHRR/METOP, (c) SEVERI/METEOSAT-MSG, (d) a microwave sensor AMSR/ADEOS, and (e) a 9-km-resolution level 4 blended product from remote-sensing system combining two microwave sensors (AMSR and TMI) and one infrared sensor (MODIS).

of these, the companion information is often available as gridded values, in the form of either quality flags or a root-mean-square error estimate associated with each value. This proviso is even

more important for level 4 products, such as primary production, where the errors of component parameters are accumulated. Moreover, many models incorporate empirical or semi-analytical

relationships based on regional datasets that cannot be extrapolated spatially. Even commonly used generic models display variable errors in space and time that users might consider.

Level 2–4 processed data are sometimes still in raw binary formats that come with external information about the data structure, but currently they are more often available in self-describing machine-independent formats. The latter are in two main formats: the HDF (Hierarchical Data Format) from the HDF Group of the University of Illinois, and the NetCDF (Network Common Data Form) from the University Corporation for Atmospheric Research (UCAR). Both are open standards and are dedicated to multidimensional gridded datasets. They come with their own software libraries; in their latest versions (HDF5 and NetCDF4), they are quite similar and have been adopted by a large number of research institutions and space agencies. Several dedicated viewers exist for both formats, and most computing platforms and programming languages, such as R, IDL/GDL, Matlab/Octave, and Ferret, include libraries for reading them. Current projects in computer science aim to define standard formats and protocol accesses to reconcile the different SRS data formats through Unidata's Common Data Model (<http://www.unidata.ucar.edu/software/netcdf-java/CDM/>).

SRS and the detection of mesoscale oceanographic features

Here, the focus is on state-of-the-art methods for detecting mesoscale oceanographic structures, such as fronts, eddies, and filaments that span spatio-temporal scales from one to hundreds of kilometres and from hours to weeks. Mesoscale structures are important ecosystem features, often associated with enhanced productivity and fish aggregation (Olson *et al.*, 1994; Bakun, 2006). They were initially studied with conductivity–temperature–depth surveys, acoustic Doppler current profilers, and ocean circulation models, then more directly and synoptically by SRS. SRS observations are also at the origin of feature-orientated regional modelling of oceanic fronts (Gangopadhyay and Robinson, 2002).

SRS for the detection of oceanic structures, using thousands of easily accessible global, daily, satellite images, is a powerful tool for studying the spatio-temporal patterns of mesoscale activity in the ocean. Several objective methods have been developed for detecting mesoscale SST frontal activity directly. The two prevailing approaches include (i) gradient-measurement and (ii) histogram-based methods.

Horizontal-gradient approaches are suited for the detection of fronts where the use of time-averaged data and a spatial resolution >4 km are appropriate (e.g. offshore fronts). Typical edge-detection methods are discrete approximations of an image-intensity-function gradient (Canny, 1986). However, gradient approximations can reveal spurious oceanic structures when applied to noisy, partially uncorrected data (Holyer and Peckinpaugh, 1989), so new gradient-based algorithms have been developed to improve front detection and preserve frontal structure using noise-reduction filters (Oram *et al.*, 2008; Belkin and O'Reilly, 2009).

The histogram-based method is the basis of the single-image edge-detection (SIED) algorithm of Cayula and Cornillon (1992), which relies on boundary detection between water masses. This algorithm is robust and distinguishes genuine ocean fronts from spurious gradients on SST images (Miller, 2009). It has been the most widely and successfully applied front-detection

method (Kahru *et al.*, 1995). The image is divided into independent subwindows, and the probability of an edge occurrence is evaluated in each subwindow by detecting bimodality in an SST histogram. The method therefore finds the threshold temperature that best separates two water masses (Cayula and Cornillon, 1992, 1995). Although the SIED algorithm performs well, Nieto (2009) improved edge detection by more than 100% in upwelling areas using sliding windows and an optimal combination of the detected segments considered as fronts, allowing the identification of most fronts in the Canary and Chilean Humboldt systems (Figure 3). In addition to gradient- and histogram-based methods, other techniques, including the entropic (Gómez-Lopera *et al.*, 2000), Canny edge detector (Canny, 1986; Castela *et al.*, 2006), and neural network approaches (Tejera *et al.*, 2002) have been applied for detecting SST fronts.

Although research has focused on thermal fronts, the detection of OC fronts has been limited (Miller, 2004; Royer *et al.*, 2004). Chlorophyll fronts arise from physical, chemical, and biological interactions within complex spatial patterns and features, such as blooms, which are more difficult to detect than SST fields (Belkin and O'Reilly, 2009); nevertheless, the same edge-detector methods can be applied. Thermal and OC fronts can also be combined into a single map for assessing biophysical interactions in specific ecosystems (Miller, 2004).

SRS data have also been used to detect mesoscale circulation features, such as filaments, eddies, and river plumes. Based on the SIED algorithm (Cayula and Cornillon, 1992), Nieto (2009) recently developed a method for identifying upwelling filaments based on their orientation and distance from the coast. Mesoscale indicators related to coastal upwelling, such as frontal intensity, filament, wind-induced turbulence, upwelling enrichment, and coastal retention indices, allow investigation of their relationships with fish abundance (Faure *et al.*, 2000). Remotely sensed SSH data provide information on sea level anomalies (SLAs) and geostrophic currents that blend pressure-gradient forces and the Coriolis force. SLA and geostrophic currents allow identification of cyclonic and anticyclonic eddies (Tew-Kai and Marsac, 2010). Indicators such as vorticity, stretch, shear, and deformation rate (Testor and Gascard, 2005) can then be computed to describe eddies. The Okubo–Weiss criterion (Okubo, 1970; Weiss, 1991) has been used widely to determine the relative contribution of distortion vs. vorticity. Finite-size Lyapunov exponents permit the detection of the Lagrangian coherent structures that cannot be detected with the Okubo–Weiss criterion (d'Ovidio *et al.*, 2004; Tew-Kai *et al.*, 2009). The eddy kinetic energy indicates the intensity of water flow and can be considered a proxy for the boundary between two eddies (Heywood *et al.*, 1994). All these indicators allow the characterization of fronts or mesoscale eddies, where the energy of the physical system is transferred to biological processes (Olson *et al.*, 1994; Bakun, 2006). Several studies have also focused on estuarine areas and associated river plumes, which constitute essential habitats sustaining part of the life cycle of coastal species, particularly the nursery grounds (Beck *et al.*, 2001). SRS data have been used to detect the spatial extents of plumes, either from the SST signature (Jiang *et al.*, 2009; Otero *et al.*, 2009) or from OC-derived properties (Molleri *et al.*, 2010). The November 2009 launch of the Soil Moisture and Ocean Salinity (SMOS) satellite, which derives salinity directly from microwave radiometer measurements (Font *et al.*, 2010), could be instrumental in detecting plume extension without using products dependent on biological processes, such as OC.

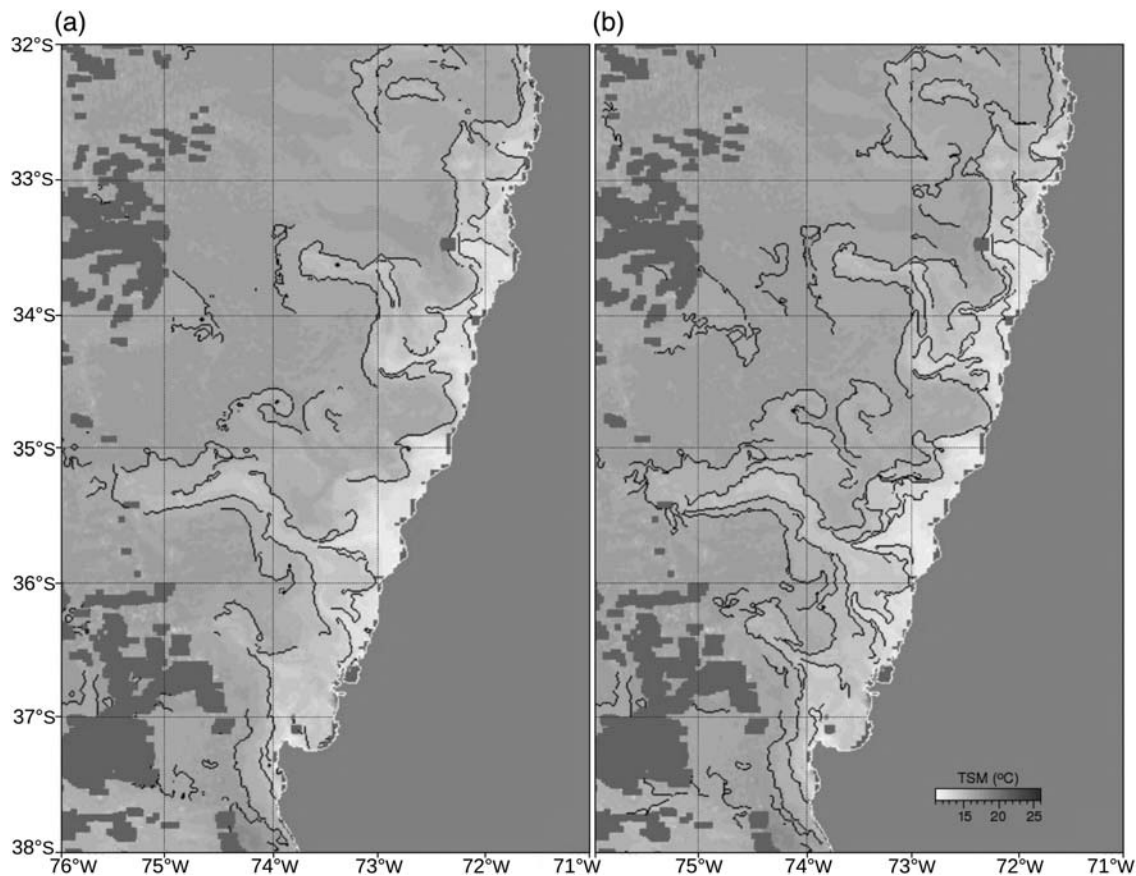


Figure 3. Example of front detection of SST in the Chilean Humboldt Current system, with land to the right, based on the (a) SIED of Cayula and Cornillon (1992) and (b) its modified version using sliding windows (Nieto, 2009). The modified algorithm allows for improving front detection by more than 100% in upwelling areas.

In summary, recent advances in satellite sensors and technology allow the scientific community access to a variety of datasets from different wavelengths of the light spectrum. These data have a global coverage at fine spatial and temporal scales and are available in open-access formats that can be imported into most statistical software. Many products have been derived from the raw satellite data, including variables such as SST, SSH, and Chl *a* concentrations. These products are being used to improve our understanding of mesoscale features important in the biological and ecological functioning of marine ecosystems. The study of mesoscale ocean features, such as fronts, filaments, eddies, Lagrangian coherent structures, and river plumes, is facilitated by a variety of techniques and algorithms that are available or under development. Detection, study, and understanding of these features is now an important component of operational oceanography and ecosystem modelling.

Identifying habitat preferences for marine fish populations

SRS measurements are the basis for a large set of indicators describing the oceanographic conditions that determine preferred habitats for feeding, spawning, maturation, and predator avoidance. The physical and biological properties of pelagic habitats influence the distribution and abundance of fish populations through environmental constraints on prey availability, the survival of larvae, and migration (Cushing, 1982; Bakun, 1996).

In addition, oceanographic conditions may influence accessibility and vulnerability to fishing by modifying gear catchability (Bertrand *et al.*, 2002). Initially used as fishery-aid products, SRS data are now essential to describing and understanding the habitats of marine species, and their relationships with oceanographic conditions.

SRS and fishery-aid products

Interest in SRS for marine fish harvesting has been recognized since the advent of satellite sensors measuring water temperature and colour in the early 1960s. Through the 1970s and the 1980s, several national scientific projects (reviewed by Santos, 2000) were conducted to (i) assess the potential of airborne and satellite oceanographic data for forecasting favourable fishing grounds, and (ii) develop distribution services to fishing vessels for remotely sensed products (Montgomery, 1981; Petit, 1991; Stretta, 1991). Support of fishing activities with public funds was advocated to facilitate the development and optimal utilization of fishery resources by decreasing fuel costs, sea time, and ship maintenance costs (Santos, 2000). Commercial products derived from satellite imagery as an aid to fish harvesting expanded rapidly and currently include SSH anomaly and OC data, in addition to meteorological and SST maps. SRS data are provided as processed datafiles in near real time (1 d to a few days from acquisition). The information is layered with computerized navigation and geographic information systems, allowing fishers to visualize maps and store data

(including their own) in a user-friendly way (Simpson, 1992). With the recognition that overfishing is a global phenomenon (Pauly *et al.*, 2003; Worm *et al.*, 2009), applied fishery research has moved increasingly from fishery-aid projects towards ecological and conservation issues, the exception perhaps being countries with developing fisheries (Solanki *et al.*, 2005).

SRS and the relationships between marine resources and oceanographic conditions

The two main ecological processes underlying the relationships between oceanographic features and marine resources in the literature are (i) prey availability, and (ii) development, growth, and survival of early life-history stages. Several studies since the 1980s have investigated the relationships between oceanographic conditions derived from SRS data and the fisheries for large and small pelagic fish, shrimps, cephalopods, and sharks in the world oceans (Maul *et al.*, 1984; Klimley and Butler, 1988; Herron *et al.*, 1989; Yang *et al.*, 1995; Bigelow *et al.*, 1999; Valavanis *et al.*, 2002; Fuentes-Yaco *et al.*, 2007; Ouellet *et al.*, 2007; Kumari and Raman, 2010). A large set of SRS indicators has been used to describe the physical properties of water masses (e.g. SST) and dynamic oceanographic features, such as eddies, filaments, and upwellings, at various spatio-temporal scales (Table 2; Lasker *et al.*, 1981; Saitoh *et al.*, 1986; Fiedler and Bernard, 1987; Demarcq and Faure, 2000). Overall, Chl *a* concentration and SST have been the most frequent indicators used to explain fish presence and abundance, generally based on catch per unit effort (cpue). Always, Chl *a* concentration, used to describe habitat productivity, was derived from Coastal Zone Colour Scanner (CZCS) and SeaWiFS data for the periods 1979–1986 and 1997–2009, respectively. SST was derived from advanced very high-resolution radiometer (AVHRR) data, which represent the most consistent time-series of SST available on a long-term and global scale. AVHRR SST products have been used to compute SST means, temporal changes, and gradients and to detect thermal fronts (Belkin and O'Reilly, 2009). Indicators describing the occurrence and dynamics of oceanic structures, such as front distance and upwelling intensity, used as early as the 1980s, recognized the strong physical–biological interactions within mesoscale features that provide favourable conditions for marine organisms (Olson *et al.*, 1994; Bakun, 2006). Methods for analysing the functional relationship between pelagic habitats and marine resources have evolved from qualitative approaches consisting of overlaying cpue data on oceanographic maps (Laurs *et al.*, 1984) to multiple linear and non-linear regression methods (Zainuddin *et al.*, 2008). However, despite the increasing complexity of statistical approaches, few studies account for spatial and temporal autocorrelations when relating gridded (e.g. Chl *a* fields) and point data (e.g. cpue). Statistical tools for analysing spatial processes are available and should be used when possible (Royer *et al.*, 2004).

Epipelagic predators, such as tuna (*Thunnus* spp.) and tuna-like species, are a particular focus of analyses involving SRS data. The strong relationship between tuna abundance and mesoscale structures such as upwelling filaments was recognized early and is explained mainly by the associated enrichment and increases in tuna prey such as euphausiids (Laurs *et al.*, 1984; Maul *et al.*, 1984; Fiedler and Bernard, 1987). Tunas are continuous swimmers, constantly seeking concentrated prey patches to satisfy their great energy requirements (Olson and Boggs, 1986). Mesoscale structures enhance productivity and forage

opportunities through complex physical mechanisms (Olson *et al.*, 1994). In particular, eddies favour the concentration and aggregation of the micronekton that constitutes the main prey of tunas (Young *et al.*, 2001; Sabarros *et al.*, 2009). Other analyses focused on the influence of oceanographic conditions on the survival of larvae based on recruitment indices, particularly in upwelling areas (Demarcq and Faure, 2000; Faure *et al.*, 2000). In such cases, the underlying processes are described by the Bakun ocean triad, i.e. enrichment–retention–concentration (Bakun, 1996, 2006). Such bottom–up control might result in non-linear dynamics (Cury and Roy, 1989); appropriate statistical methods, such as generalized additive models, need to be used accordingly (Faure *et al.*, 2000).

SRS and preferred habitats during migrations

The field of biologging, the deployment of recording and transmitting tags on animals to study their movements, behaviour, physiology, and habitat usage, has expanded rapidly over the past decade with the advances in miniaturization of electronic tags (Bograd *et al.*, 2010). SRS oceanographic data combined with tracking data can greatly increase our understanding of an animal's habitat and behaviour. SRS data provide both the meso- and larger-scale oceanographic context for each available animal position and time. The types of SRS data most commonly used with animal tracking include SST, surface Chl *a*, and geostrophic currents. Before linking tracking and SRS data, it is preferable to estimate the most likely tracks using a state–space modelling approach (Patterson *et al.*, 2008). In addition, improved tag position data are obtained by including satellite-derived SST in the estimation process (Nielsen *et al.*, 2006). A recently developed alternative modelling approach validated with GPS data consists of bootstrapping random walks generated from the probability distributions of animal locations and trajectories for the geolocation of tagged animals (Tremblay *et al.*, 2009). The method provides a flexible framework for including remotely sensed datasets and has the advantage of being easier to implement than the state–space models.

SSTs are the most common SRS data used in combination with tagging data. These can be analysed to determine whether an animal uses mesoscale features, including temperature fronts and cyclonic eddies, and to characterize its habitat in terms of preferred SSTs (Polovina *et al.*, 2000; Kobayashi *et al.*, 2008). For loggerhead sea turtles (*Caretta caretta*), preferred habitat north of Hawaii constitutes a temperature and chlorophyll front delineated by a value of SST of 18°C. Daily maps of probable turtle habitat, defined by a narrowband around the 18°C SST isotherm, are distributed to longline fishers to help them avoid the area to reduce turtle bycatch (Howell *et al.*, 2008).

SRS chlorophyll data often serve as a valuable proxy for water mass boundaries and may identify upwelling associated with mesoscale features (see section on detecting these features). The range of surface chlorophyll values used by an animal may help characterize its habitats (Polovina *et al.*, 2000; Kobayashi *et al.*, 2008). For example, by combining turtle tracking with SeaWiFS chlorophyll data, Polovina *et al.* (2001) characterized and described interannual changes in the position and dynamics of a North Pacific basin-wide chlorophyll front, the Transition Zone Chlorophyll Front (TZCF), which has proven to be an important migration and forage habitat for a variety of species.

Geostrophic currents can be estimated from satellite altimetry and are especially useful in identifying major ocean currents,

mesoscale eddies, and meanders (Polovina *et al.*, 2006; see section on mesoscale structures). For example, SRS chlorophyll and altimetry together provided insight into the importance of the Kuroshio Extension Current as a key forage habitat for juvenile loggerhead turtles (Polovina *et al.*, 2006). When sufficient tracks are available, SRS oceanographic and tracking data can be integrated in statistically rigorous ways. For example, one approach to defining an animal's habitat begins by selecting a number of relevant environmental variables. Then, for each variable, statistical tests are conducted to determine whether the frequency distribution occupied by the animal is statistically different from the distribution constructed from an envelope around its track (Kobayashi *et al.*, 2008). For variables with significant differences between the two distributions, it can be inferred that the animal is selecting a subset of the available range of values; that subset is then used to define its habitat (Kobayashi *et al.*, 2008). A second statistical approach determines whether an animal is actively associating with an ocean feature, such as an eddy or front. This approach constructs the frequency distribution of the distance between the animal and the feature for all available animal positions. A randomization test then determines whether this distance is statistically significant (Kobayashi *et al.*, 2011).

In summary, understanding and identifying habitat preferences is crucial to management and conservation of marine populations. Initially used as fishery-aid products, SRS data provide an invaluable source of information for unveiling the relationships between marine resources and oceanographic conditions. Since the advent of SRS data acquisition, many studies have focused on the impact of the physical environment on marine species through the relationships between physical indicators and prey availability, and the development, growth, or survival of early life stages. The relationship between thermal fronts and the location of large pelagic species has been demonstrated since the early 1980s. SRS data also cover a wide range of applications for improving our knowledge of marine species ecology, in particular their movements and migrations. The combination of data collected by electronic tags and SRS-derived oceanographic data has improved our understanding of the impact of oceanic features on marine species' behaviours while foraging and migrating.

SRS data for ecosystem analyses and models

SRS and ocean partitioning

An ecosystem can be defined as a system of complex interactions of populations between themselves and their environment (Garcia *et al.*, 2003). The first step in any EAFM is the definition of the spatio-temporal extent of the system of interest. A major objective of the discipline of biogeography is to investigate the structure, composition, and links between different ecosystems of interest to regroup them at larger scales (Lomolino *et al.*, 2005). Consequently, biogeography requires a lot of data that are homogeneously distributed in space and time (Ducklow, 2003). Because of the dynamic nature of the oceanic realm and logistic difficulties of sampling the marine environment (Richardson and Poloczanska, 2008), advances in marine biogeography have been constrained by data availability and coverage (Longhurst, 2007). Several attempts have been made in the past century to partition the global ocean using biological observations (Ekman, 1953; Margalef, 1961) and physical variables (Cushing, 1989; Fanning, 1992). It was only in the mid-1980s that Yentsch and Garside (1986) suggested that major oceanographic patterns might be

approximated by the primary production derived from satellite observations. Based on this hypothesis, the CZCS dataset and parameters known to control algal blooms were used to implement a methodology for defining ecological units (Sathyendranath *et al.*, 1995). Subsequently, Longhurst *et al.* (1995) proposed partitioning the global ocean into four biomes, subdivided into ~50 biogeochemical provinces (BGCP), each province representing an ecological entity with specific and predictable environmental conditions.

During the past decade, Longhurst-type partitioning has been the dominant paradigm in marine biogeography. Several analyses have questioned the relevance of BGCP by focusing on physical conditions and particular components of the pelagic foodweb, i.e. *in situ* temperature and salinity (Hooker *et al.*, 2000), bacterial abundance (Li *et al.*, 2004), plankton abundance, composition, and diversity (Gibbons, 1997; Beaugrand *et al.*, 2002; Alvain *et al.*, 2005), surface ocean Chl *a* (Hardman-Mountford *et al.*, 2008), and the distribution of top predators (Fonteneau, 1998). Overall, results revealed a good match between the spatio-temporal distribution and composition of marine organisms and Longhurst's provinces. The emergent hypothesis was that the physiological and behavioural characteristics of marine organisms were adapted to their ecological provinces; the physical and biogeochemical environment may constrain the abundance and production of lower trophic levels in ways that affect the entire foodweb (Beaugrand *et al.*, 2002). The use of ecological provinces has been proposed as a useful tool for time-series analysis, management, and conservation planning at global scales (Pauly *et al.*, 2000). Alternative partitions have also been proposed for economic and conservation applications in coastal regions (Spalding *et al.*, 2007; Sherman *et al.*, 2011). Always, however, static partitioning appears too simplistic for operational management of the dynamic marine environment, which can respond quickly to changes in physical forcing (Platt and Sathyendranath, 1999; Cullen *et al.*, 2002). Recent work, based on SRS data in conjunction with other datasets, has attempted to implement dynamic biogeography at regional scales (Devred *et al.*, 2007; G. Reygondeau, pers. comm.; Figure 4). These methods display promise in tracking spatial changes in ecosystem boundaries and might eventually be able to delineate regions displaying early signs of anthropogenic pressures requiring management measures. The use of biogeography as a spatial reference to identify and monitor specific ecosystems appears to be a useful tool for ecosystem management and biodiversity conservation (Pauly *et al.*, 2000).

SRS and ecosystem carrying capacity

The relative role of top-down (consumer-driven) and bottom-up (resource-driven) controls in regulating animal populations and structuring ecosystems has been a subject of debate among ecologists for some time. Pacific-Atlantic cross-system comparisons reveal evidence of bottom-up control through the dependence of long-term fishery production on SRS-derived phytoplankton production (Ware and Thomson, 2005; Frank *et al.*, 2006; Chassot *et al.*, 2007). At global scales, i.e. across large marine ecosystems (LMEs), SRS-derived estimates of primary production are also related to fisheries catches (Chassot *et al.*, 2010; Sherman *et al.*, 2011). The relationship between primary production and catches is complex and varies among LMEs; a large portion of the variance results from differences in life histories (and hence productivities) of fish (as indexed by maximum length), ecosystem

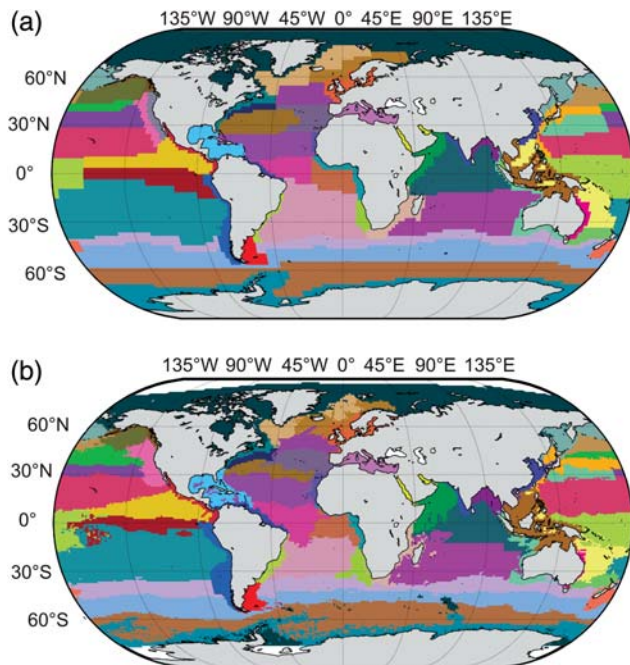


Figure 4. (a) Map of Longhurst (2007) BGCP, and (b) a map of the dynamic BGCP for 2005. Dynamic BGCP were derived from SST based on the AVHRR series, SeaWiFS Chl *a*, salinity (World Ocean database), and bathymetry (GEBCO) datasets (G. Reygondeau, pers. comm.).

type, and fishing pressures (Chassot et al., 2010). Ecosystems fished at unsustainable levels are less efficient at converting primary production into fisheries catches, and the exploitation of small-bodied (lower trophic level) fish increases the catch per unit of primary production. The importance of the potential link between primary and fisheries production was realized more than half a century ago, but the recent detailed exploration of this issue was only made possible by the advent of SRS OC and primary productivity. Past large-scale studies relied on *in situ* datasets resulting from different sampling and processing methods and were generally characterized by low spatio-temporal sampling coverage. SRS of the marine environment is now basic to cross-trophic-level analyses of ecosystem production, structure, and function only because of the availability of a comprehensive, fine-scale, and consistent sampling framework (Platt et al., 2007).

SRS and ecosystem models

Ecosystem models are considered a necessary part of EAFM implementation (Cury et al., 2008). Estimation of primary production is common to most modelling approaches, as an integral part of the model, or as a forcing function. Primary production is a typical level 4 SRS product requiring the use of non-SRS parameters, such as mixed-layer depth and photosynthetically active radiation, in addition to SRS Chl *a* (and often SST) in a model (Longhurst et al., 1995; Behrenfeld and Falkowski, 1997). SRS-derived primary production has been used as an initial forcing at the base of the modelled foodweb to investigate energy transfers from lower to upper trophic levels. For instance, an Ecopath with Ecosim model was applied to the eastern tropical Pacific to explore the effects of climate change on open-sea

communities (Watters et al., 2003). Further, size-spectrum modelling approaches have been used to estimate fish production and biomass in the absence of fishing, based on satellite-derived primary production allocated to phytoplankton weight classes to track energy fluxes through marine foodwebs at a global scale (Jennings et al., 2008). These size-spectra approaches, coupled with SRS Chl *a* and SST data, have great power for exploring the relative impacts of fishing against an unfished baseline at an ecosystem level (Jennings and Blanchard, 2004), as well as elucidating biogeochemical processes (Wilson et al., 2009).

An alternative approach is to estimate primary production using coupled physical–biogeochemical models (for a review, see Plagányi, 2007). This has the potential for reconstructing past (pre-SRS) and forecasting future ocean states, in particular to addressing the potential effects of climate change. However, SRS products are again essential, for either model initialization, parameter estimation of the biogeochemical model from OC data (Friedrichs, 2002; Huret et al., 2007), or assimilation into operational systems. To date, the latter has happened only with SST and SSH (Cummings et al., 2009). As biogeochemical and ecological considerations are incorporated into ocean data assimilation systems (Brasseur et al., 2009), different SRS products, allied with automated *in situ* data, will become a major source of information for these operational systems and will help meet the challenges of an EAFM.

To conclude, the complexity of marine ecosystems and the large spatio-temporal scales involved in their functioning are difficult to grasp using point and regional observations. SRS provides daily high-resolution data at global scales not feasible by any other means. Such a synoptic view has allowed ocean partitioning based on objective physical and biological criteria and specific functioning. The continuing daily production of satellite images can also be used to track temporal variations in the marine provinces and to predict how their structure and spatial extent might be affected by climate change. SRS data and their derived products, such as temperature and primary production, are also invaluable sources of information as inputs to ecosystem models that are fully part of the implementation of an EAFM.

Discussion

Computing SRS-derived indicators for fishery science

SRS data have been used in fishery science since the availability of the first SST and colour datasets at the end of the 1970s. Over time, the diversity and the resolution of datasets and SRS-derived indicators have increased, allied with our understanding of the complex spatio-temporal relationships between oceanographic conditions and individual, population, and community dynamics (Polovina and Howell, 2005). However, most of the published papers reviewed here rely on short time-series of data and relatively few remotely sensed indicators: SST and primary production derived from AVHRR and SeaWiFS sensors, respectively. Some recent studies included indicators derived from several SRS sources and use non-linear statistical models (Zainuddin et al., 2008; Tew-Kai and Marsac, 2010). New indicators have been proposed to characterize the oceanographic features involved in the ecological processes determining fish distribution and occurrence, e.g. for feeding and spawning; these include the duration of spring blooms, the size composition of phytoplankton, and the degree of persistence and recurrence of oceanic structures (Palacios et al., 2006; Platt and Sathyendranath, 2008). These indicators aim to

describe better the ecological processes of interest, e.g. for northern pink shrimp (*Pandalus borealis*), they elucidate the mechanisms governing egg hatching times and recruitment in the North Atlantic (Koeller *et al.*, 2009). Although the period for which SRS data are available now spans 12 and 30 years for Chl *a* and SST, respectively, few studies deal with such temporal scales. However, longer periods with contrasting environmental conditions and fish abundance are required to derive robust relationships between oceanographic features and the population dynamics of marine species. Future studies should also account better for the spatial dimension of satellite SRS data by making use of appropriate geostatistical methods.

Different satellites, sensors, processing techniques, and models can be used to compute SRS indicators. Comparative analyses of remotely sensed Chl *a* and depth-integrated primary production derived from different models and sensors have revealed large differences in processed data on both global and regional scales (Carr *et al.*, 2006; Friedrichs *et al.*, 2009; Djavidnia *et al.*, 2010). However, throughout the literature reviewed, sensitivity analyses were never conducted to assess the robustness of the relationships relative to the method used to compute the various indicators. In addition, information on the uncertainties associated with SRS-processed data, e.g. standard deviation around Chl *a* (Mélin, 2010), was never provided, and remotely sensed indicators were always treated as data measured without error. Although cpue was used to describe marine population abundance, such data are often fraught with uncertainty and might not reflect fish abundance accurately, particularly for pelagic species (Hilborn and Walters, 1992). Future studies using SRS data should recognize all sources of uncertainty associated with SRS and population-abundance indicators and should evaluate the sensitivity of results to the uncertainty in input parameters.

Including the vertical dimension in SRS approaches

SRS data have been used mainly to describe surface environmental conditions, but to detect SRS Chl *a* and water turbidity might be more relevant, because they account better for the vertical dimension of fish habitats (Brill and Lutcavage, 2001). Recently, Takano *et al.* (2009) developed an empirical method to estimate the three-dimensional structure of physical features in time and space based on satellite altimetry data and *in situ* temperature and salinity profiles. The method demonstrated good agreement between observed and estimated isothermal depths and was useful for predicting the vertical habitat utilization of bigeye tuna (*Thunnus obesus*).

In open-ocean ecosystems, pelagic environmental conditions derived from SRS often reflect prey distribution and abundance that are generally poorly known and difficult to monitor. Information on mid-trophic-level prey in open-ocean ecosystems can be collected from (i) scientific trawl and acoustic surveys, (ii) information on the diet of predators that can be used as biological samplers of micronekton, and (iii) outputs from end-to-end ecosystem models. Investigating the relationships between SRS-derived oceanographic conditions and prey might then provide useful insights into predator habitat preferences.

Ecosystem models that use SRS and *in situ* data as inputs include the vertical dimension and overcome the limitations of surface-restricted SRS data. SRS data have now become a major source of information for ocean observation programmes, such as

the Global Ocean Observing System (GOOS), necessary for operational oceanography in an EAFM context. A better understanding of ocean dynamics from environment to fisheries at a global scale requires the ability to combine data collected with a wide range of sensors, both *in situ* and remote, deployed on both mobile and stationary platforms. The development of common data formats and access protocols, such as SensorML (see <http://www.opengeospatial.org/projects/groups/sensorweb>), is instrumental in addressing these issues.

Studies combining SRS-detected mesoscale structures with three-dimensional ocean circulation models may also further understanding of the physical mechanisms involved in the generation of oceanographic features, such as eddies and meanders, and the associated enhanced productivity (Kurien *et al.*, 2010).

SRS and fisheries management

In the context of an EAFM, SRS of the marine environment provides a valuable source of information on the interactions between fish species and their environment. Including environmental effects on fish catchability, abundance, and distribution in the process of abundance index estimation would be a first step to improving scientific advice on the state and management of fish stocks. Identifying spawning and/or feeding grounds based on SRS is also a prerequisite for spatially orientated management measures, such as the implementation of marine protected areas (Druon, 2010). In the Pacific, the Hawaii-based swordfish (*Xiphias gladius*) longline fishery was closed in 2006, because of excessive bycatch of loggerhead sea turtles. Knowledge of turtle habitats gained from tracking and SRS data (see above) was used to assist fishers in avoiding areas with high turtle bycatch. Launched in 2006, TurtleWatch provided 3-d SST composite maps and weekly ocean currents estimated from SRS altimetry for the fishing ground and the region with the highest probability of loggerhead and longline gear interactions (Howell *et al.*, 2008; Figure 5). TurtleWatch was revised in 2008, based on experience with the product in 2007, feedback from fishers, and analysis of 2007 fishery and bycatch data; revisions reflect the temporally dynamic feature of the high-bycatch zone.

The ability to track and predict the spatial dynamics of marine species using key environmental parameters will likely become increasingly important as climate change alters phenological and geographical distribution patterns of many marine populations (Planque *et al.*, 2010). Consequently, many habitat and niche models have been developed in the past few years to depict and predict the spatial distribution and temporal fluctuations of key-stone species. Environmental-niche models attempt to reproduce the current distribution and temporal fluctuations of a given species by estimating suitable physical and biological conditions. SRS constitutes an essential data source for niche- and habitat-model implementation by providing worldwide coverage at high temporal resolutions of key environmental parameters (e.g. temperature) affecting marine organisms. Chl *a* is currently the only biotic parameter monitored at the macroscale; consequently, several studies have attempted to include it in the environmental-niche models (Polovina *et al.*, 2001). However, because of several inherent biases in SRS data, this remains a challenging task (Reygondeau and Beaugrand, 2011). Recently, Cheung *et al.* (2009, 2010) used the model outputs derived from post-processed SRS data to predict the effects of climate change on marine biodiversity and on maximum fisheries catch potential under some Intergovernmental Panel on Climate Change (IPCC) scenarios.

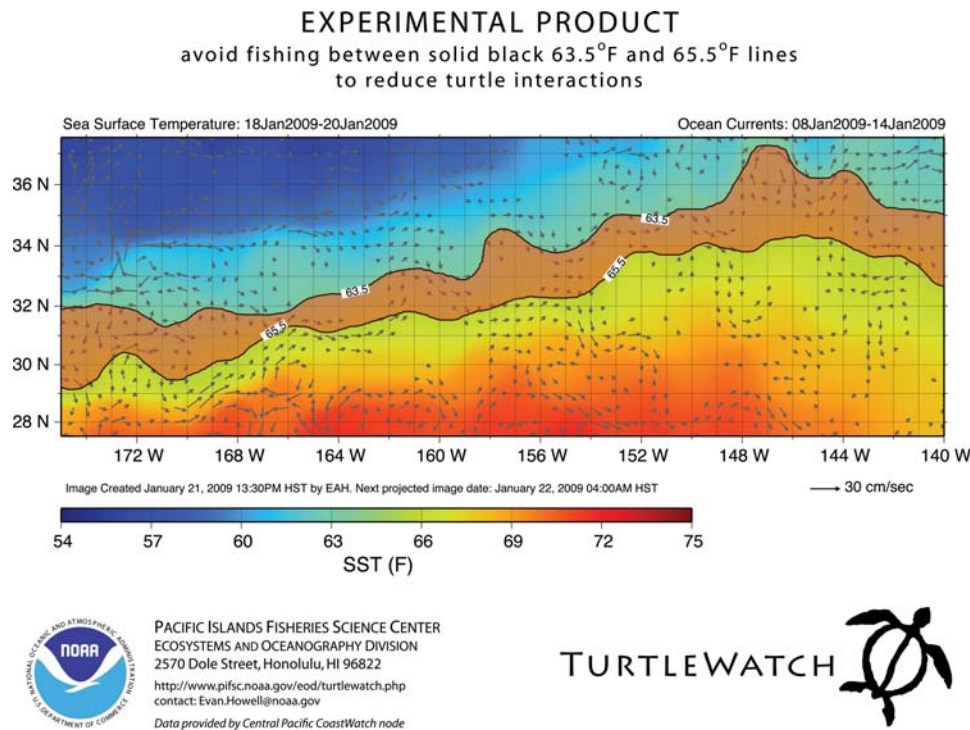


Figure 5. Example of the TurtleWatch mapping product identifying the region with the highest probability of loggerhead turtle and longline gear interactions, distributed daily in near real time to fishers. The area with the highest probability of loggerhead bycatch that fishers should avoid (delineated by solid black lines) represents the area between the 63.5 and 65.5°F SST isotherms.

Such approaches could help implement adaptive fisheries management plans that respond to the predicted changes in the spatial distribution and productivity of fish populations.

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