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Alternative attractors in marine ecosystems: A comparative analysis of fishing effects

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ABSTRACT

With the aid of *Ecopath with Ecosim* mass-balance model and perturbation by fishing, the existence of alternative attractors in marine ecosystems was explored. The ecosystem was investigated in the form of bottom-up, mixed and top-down control, respectively. Furthermore, fishery species were changed from wasp-waist to top predators. Thus, the effect of the trophic level to the existence of the alternative attractors was showed. The results proved that there were indeed alternative attractors in the studied ecosystems, and alternative attractors might be easier to appear from the systems with top-down control. As the fishing trophic level changed, the occurrence frequency of the alternative attractors changed slightly, but the models with alternative attractors changed significantly.

1. Introduction

The idea of alternative attractors existing in ecological systems was first proposed in the 1960s (Lewontin, 1969) with a simple question: "Can there be more than one stable community in a given habitat?" Simple abstract theoretical models (Holling, 1973; Noy-Meir, 1975; Glipin and Case, 1976; May, 1977; Case and Casten, 1979; Law and Morton, 1993) have shown that alternative attractors are plausible and indeed might be the common features in ecosystems (Knowlton, 2004), but they are rarely existed in more complex ecological models (Janse, 1997; van Nes et al., 2002, 2003). van Nes and Scheffer (2004) showed that the alternative attractors might appear robust from interactions between large number of species in response to gradual environmental change or evolution. The existence of alternative attractors in ecosystems has some important influence on restoration ecology (Scheffer et al., 2001; Suding et al., 2004) and conservation of marine ecosystems (Knowlton, 2004). The ecosystems with alternative attractors often show catastrophic shifts and may cause large losses of ecological and economic resources (Scheffer et al., 2001). Furthermore, it requires drastic and expensive intervention to restore the system to a desired state (Maler, 2000).

In oceanography (Steel, 1998, 2004; Rothschild and Shannon, 2004), 'regime shift' is often used in describing abrupt shifts in marine ecosystems. Generally speaking, there are three different types of regime shifts (Collie et al., 2004). The first is a smooth regime shift, which is characterized by a quasi-linear function between the forcing and responsible variables (Fig. 1a). The second is an abrupt shift, which is presented by a nonlinear relationship between the forcing and the response variables (Fig. 1b). The last is a discontinuous regime shift, which involves an abrupt response between alternative attractors (Fig. 1c). In a nutshell, alternative attractor is

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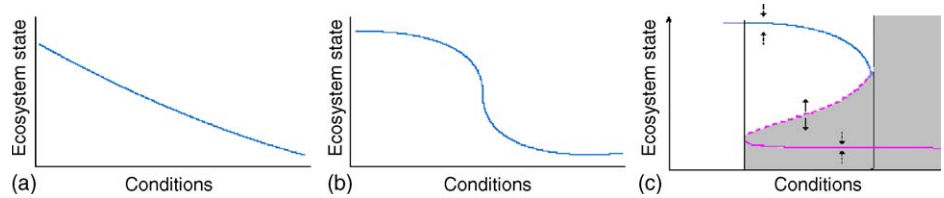

Fig. 1 – Three different types of regime shift: (a–c) smooth, abrupt and discontinuous. Alternative attractors exist in systems with different basin of attraction (c). The stable states are given by solid line and the dashed line is the unstable states. The grey shaded area shows the basin attraction of the lower stable state and the other area (except the dashed line) shows the basin attraction of the upper stable state (figure modified from Scheffer and Carpenter, 2003; Schroder et al., 2005).

a discontinuous regime shift which means that ecosystem has different basins of attraction under the same external environmental conditions (Schroder et al., 2005). When the external force perturbs the ecosystem, the system state will transit to the other different stable state.

Although the concept of the alternative attractors is straightforward, understanding and identifying it has proven to be difficult (deYoung et al., 2004). Scheffer and Carpenter (2003) presented that alternative attractors were not easy to be found empirically. However, the recent field studies have provided strong proofs of the existence of alternative attractors in ecosystem. Examples include shallow lakes (Scheffer et al., 1993; Morris et al., 2003), benthic pond food webs (Chase, 2003) and marine ecosystems. Marine ecosystems were among the first to provide potential examples of alternative attractors (Knowlton, 2004). For example, coral reef communities exhibit two alternative states. One is dominated by corals and the other is dominated by seaweeds (Done, 1991; Knowlton, 1992; Hughes, 1994); rocky initertidal and subtidal habitats have also been described as examples of alternative attractors (Johnson and Mann, 1988; Dudgeon and Petraitis, 2001). Soft sediment communities may probably cause alternative attractors, in which one state is dominated by ghost shrimp and the other by bivalves or phoroids (Petersen, 1984).

Until now, most of the oceanographers have taken a mainly empirical approach to identify the alternative attractors by testing the time series of biotic and abiotic variables (Collie et al., 2004). Scheffer and Carpenter (2003) presented a set of criteria for detecting alternative attractors, which can be expressed as three questions (Collie et al., 2004). Here we use one of the three criteria for diagnosing the existence of alternative attractors. The question is listed as follows:

> *Does the system switch to an alternative state when perturbed?* A positive answer to this question indicates the existence of alternative attractors. With the help of the *Ecopath with Ecosim* (*EwE*) model, we can use this criterion to find whether there are different stable states in marine ecosystems or not.

It is clearer that the interactions (e.g. predation and competition) in marine ecosystem have much more important influence on driving oceanic community dynamics than what has been previously thought (Verity and Smetacek, 1996). Predation and competition between interspecific and intraspecific play an important role in keeping the structure and function of the ecosystem. Furthermore, these interactions will significantly affect the occurrence of the alternative attractors (van Nes and Scheffer, 2004). Cury and Shannon (2004) showed that different control mechanisms could trigger the regime shifts in marine ecosystems. Gragnani et al. (1999) presented that changing the fishing predation on the phytoplankton would cause the ecosystem to different stable state. One key feature of Ecosim is its ability to allow exploring the implications on system dynamics with different views on how the biomass of different groups in ecosystem is controlled. Therefore, we will test the effect of the control mechanism on the existence of alternative attractors in ecosystem with the *EwE* model from a different view.

Fisheries can affect the entire food chain, causing profound variation in species abundance on various tropic levels (Cury, 2000; Reid et al., 2000). Furthermore, fishing was used as an indication of perturbation to investigate the alternative attractors in Georges Bank haddock, *Melanogrammus aeglefinus* (Collie et al., 2004). Fisheries, exploiting the wasp-waist species and occurring at intermediate trophic levels, have a potential disrupting effect on the stability of marine ecosystems (Vasconcellos et al., 1997). Therefore, we change the fishery species from wasp-waist to top predators with fishing mortality as a perturbation to marine ecosystems to test whether there are alternative attractors or not with the diagnosing criterion.

So, the first purpose of this paper is to test the existence of alternative attractors in marine ecosystems, and then we will survey the effect of different flow in control mechanism and the trophic level on the existence of alternative attractors with the aid of the *EwE* mass-balanced models.

2. Material and methods

2.1. *The Ecopath with Ecosim approach*

Ecopath with Ecosim is a dynamic simulation tool developed for straightforward construction, parameterization and for the analysis of mass-balance trophic models of aquatic and terrestrial ecosystems (Christensen and Walters, 2004). *EwE* is a free ecological/ecosystem modeling software suite. It can be used to address ecological questions and to evaluate ecosystem effect of fishing and model effect of environment changes. Many application examples of *EwE* can be found at http://www.ecopath.org. The formulations and concepts are listed on this web page, and we just summarize the general approach from it.

The main inputs for each group are production (P), biomass (B), diet matrix, ecotrophic efficiency (EE) and the consumption (Q) rates. Trophic mass-balance models in *EwE* rely on a system of linear equations which represent each of the functional groups in the ecosystem, and describe the balance between biomass gains through production and losses, involving predation, fishing and other exports. The basic equation of *EwE* is expressed as follows (Christensen and Walters, 2004):

$$B_i \left(\frac{P}{B}\right)_i EE_i - \sum_{j=1}^{n} B_j \left(\frac{Q}{B}\right)_j DC_{ji} - EX_i = 0 \quad (1)$$

where B_i is the biomass of the prey functional group *i* in a given period of time; $(P/B)_i$ is the production/biomass ratio for prey *i*; EE_i is the ecotrophic efficiency (the fraction of production consumed, fished or exported out the system); EX_i is the fishing yield for *i*; B_j is the predator biomass *j*; $(Q/B)_j$ is the consumption/biomass ratio for predator group *j*; DC_{ji} is the fraction of *i* in the diet of *j*. The Ecopath equation as differential format is (Espana, 2003):

$$\frac{dB_i}{dt} = f(B) - M_0 B_i - F_i B_i - \sum_{j=1}^{n} c_{ij}(B_i, B_j) \quad (2)$$

where $f(B)$ is a function of B_i if *i* is a primary producer, or $f(B) = g_i \sum_{j=1}^{n} c_{ij}(B_i, B_j)$ if *i* is a consumer, $c_{ij}(B_i, B_j)$ is the function to predict Q_{ij} from B_i and B_j; M_0 is the mortality rate not accounted for consumption in the system; F_i is the fishing mortality. When dB_i/dt equals to zero, then the system lies at the equilibrium state.

2.2. General method

In this section, we will describe the general method to scan the alternative attractors in marine ecosystems with the fishing (F) as the perturbation. First, the F was kept in baseline values for 20 years so that the system can sustain the stable state. Then, a fishing pattern was chosen which would generate a five-fold increase of F during $t_1 - t_2$ time interval (here 10 years). Finally, the fishing mortality F returned from time t_2 to the baseline and the system would run for another 70 years to test whether the system recovers to their original state or not (Fig. 2). When the system reached the other stable state, there will be alternative attractors in the studied model based on the diagnosing criteria. Otherwise, there will be no alternative attractors. During our simulations, there are general two types of attractors: point attractor and cyclic attractor. Point attractor means that the system state attains an equilibrium point, and if the system has become cyclic, the state is a cyclic attractor. So, there are two general cases of state transition: (i) point attractor to point attractor (2P) and (ii) point attractor to cyclic attractor (P–C).

We used 26 marine ecosystems to test the existence of the alternative attractors (see Table 1), and there are total 36 mass-balance models for the studied ecosystems. It should be noted that for several ecosystems studied, more than one model is considered (i.e. two different time periods are considered for Eastern Scotian Shelf, so there are two mass-balance models for Eastern Scotian Shelf ecosystem).

Six scenarios were run for each of the 36 models: these were two test cases (F of the predator at a high trophic level given in Table 1 for each model, and F of the intermediate trophic level fish species in each model, Table 1) and each

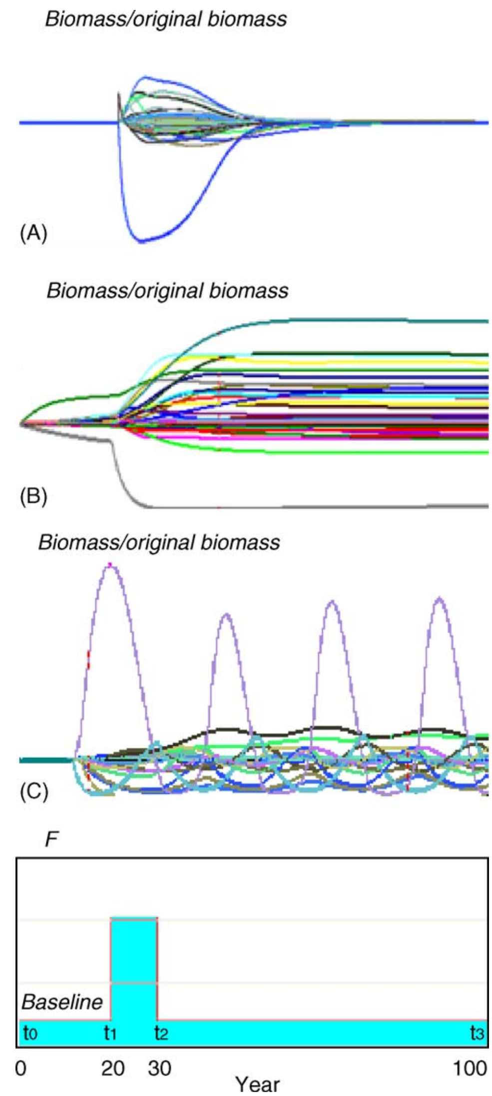

Fig. 2 – Simulation of marine ecosystem after fishing perturbation imposing a five times increase in fishing mortality F. t_0 is the start time of the simulation with the F baseline; $t_1 - t_2$ is the time interval when fishing mortality was kept under a higher value (here 10 years); interval $t_2 - t_3$ corresponds to the system recovery time. The time of t_3 is 100 years. Three different simulation results are presented. One is that the ecosystem recovered completely to their original state after the 10 years perturbation (A), the other is that the ecosystem attains a different stable state after the perturbation (B) and the third is that the system dynamics reaches a cyclic state (C).

Table 1 – Models used for analyses of alternative attractors in marine ecosystems

Marine ecosystem	Group		TL		F[a]	
	Top	Inter	Top	Inter	Top	Inter
Weddell Sea (Jarre-Teichman et al., 1997)	Mammals	Pisces	4.14	3.05	0.001	0.001
Darwin Harbour[b]	Pelagic fish	Benthic fish	3.96	3.01	0.16	0.01
South East Shelf[b]	Dories	L Benthic crusts	4.57	2.92	0.01	0.01
Bight coastal ecosystem[c]	Large pelagic fish	Catfish	3.9	2.2	0.015	0.004
Caete mangrove estuary[d]	Predatory fish	Shrimps	4	2.52	0.1	0.3
Eastern Scotian Shelf—1980s[e]	Grey seals	Shrimp	4.16	2.45	0.0002	0.0035
Eastern Scotian Shelf—1990s[b]	Grey seals	Shrimp	4.36	2.45	0.1	0.1
Grand Banks of Newfoundland—1900s[b]	Harp seals	Small Mesopelagics	4.13	3.38	0.1	0.1
Grand Banks of Newfoundland—1980s AB[e]	Cod > 35cm	Large Crustacea	4.17	2.93	0.67	0.02
Grand Banks of Newfoundland—1980s SH[f]	Harp seals	Lobster	4.24	2.93	0.02	0.32
Grand Banks of Newfoundland—1990s[f]	Harp seals	Lobster	4.27	2.93	0.044	0.32
Northern Gulf of St. Lawrence—1980s[g]	Harp seals	Large crustacean	4.15	3.01	0.016	0.05
Southern Gulf of St. Lawrence—1980s[b]	Harp seals	Large crustacean	4.04	2.83	0.003	0.09
Bohai Sea (Tong et al., 1999)	Top pelagic	Herbivorous feeders	4.18	2.17	0.15	0.1
Faroe Islands—1997 (Zeller and Reinert, 2004)	Tooth mammals	Benthos	4.67	2.51	0.062	0.002
Bay of Biscay—1998[b]	Large pelagic	Small Pelagic	4.07	2.75	0.06	0.0016
Moorea Fringing Reef[h]	Fish pisci1	Fish herbi	3.47	2	0.001	0.001
Floreana rocky reef (Okey et al., 2004)	Pelagic predators	Detritivorous fish	3.86	2.12	0.22	0.62
Guinea—1998[b]	Gros capitaine	Mulets	4.07	2.32	0.37	0.04
Iceland—1950 (Natoumbi Mendy, 1999)	Toothed whales	Herring	4.07	2.9	0.003	0.18
Iceland—1997 (Natoumbi Mendy, 1999)	Toothed whales	Herring	4.07	2.9	0.003	0.18
Mauritania EEZ—1987[b]	Selaciens L pred	Crustaces comm.	4.36	2.71	0.01	0.02
Mauritania EEZ—1998[b]	Selaciens L pred	Crustaces comm.	4.45	2.71	0.01	0.02
Tamiahua Lagoon (Abarca-Arenas and Valero-Pacheco, 1993)	O. saurus	Shrimp	3.44	2.66	0.01	0.001
Laguna de Bay—1968 (Delos Reyes, 1993)	MUDFISH	Shrimp	3.09	2.46	2.04	30.61
Laguna de Bay—1980 (Delos Reyes)	MUDFISH	Shrimp	3.06	2.46	0.7	0.68
San Miguel Bay (Bundy, 2004)	LP	Pen	4.14	2.61	1.4	1.3
Azores—1997 (Guénette and Morato, 2001)	Pagellus bogaraveo	Coastal M herb	4.17	2.12	0.3	0.03
Northern Benguela—1970s[i]	Hake	Anchovy	3.43	2.44	1.732	1.092
Northern Benguela—1980s[i]	Hake	Anchovy	3.55	2.8	1.676	0.732
Northern Benguela—1990s[i]	Seals	Macrobenthos	4.3	2.11	0.01	0.013
Chiku lagoon (Lin et al., 1999)	Pisci. fish	Oyster	3.55	2.1	0.86	0.64
Prince William Sound[j]	Halibut	Dult Herring	4.53	3.1	0.1	0.9
Prince William Sound (Old)[j]	Demersal fish	Epi. Zoobenthos	3.92	2.9	0.04	0.14
USA, Mid Atlantic Bight (Okey, 2001)	Goosefish	Shrimp	4.36	2.41	0.28	0.004
West Florida Shelf (Okey et al., 2004)	LgOcePisc	Adult Shrimps	4.7	2.89	0.03	0.03

TL: trophic level.

[a] *F*, baseline (per year) refers to the species' fishing mortality used in the corresponding marine models.
[b] Models were from http://www.ecopath.org.
[c] Gasalla and Rossi-Wongtschowski (2004).
[d] Wolff et al. (2000).
[e] Bundy (2002).
[f] Heymans et al. (in press).
[g] Morisette et al. (2003).
[h] Arias-Gonzalez et al. (1997).
[i] Shannon et al. (2004).
[j] Kline and Pauly (1998).

test was run under three different flow control scenarios: top-down, mixed and bottom-up. The three control types are: (i) bottom-up control, (ii) mixed-control and (iii) top-down control. A detailed description of the different control types is listed in Christensen et al. (2002).

Top predators and wasp-waist species are used, respectively, as fishing group. The criteria for choosing the two groups in a marine ecosystems model must occupy an appropriate trophic level and already be fished in *EwE* model (Vasconcellos et al., 1997).

3. Results

When the control mechanism is bottom-up, there are no alternative attractors in the studied ecosystems no matter which group (top trophic or wasp-waist tropic level) is fished. That is to say that the quantity of all the species in the studied models will return to the same stable state after the perturbation (Fig. 3a and b). There is only one same point attractor (1P) in the studied mass-balanced model (Table 2).

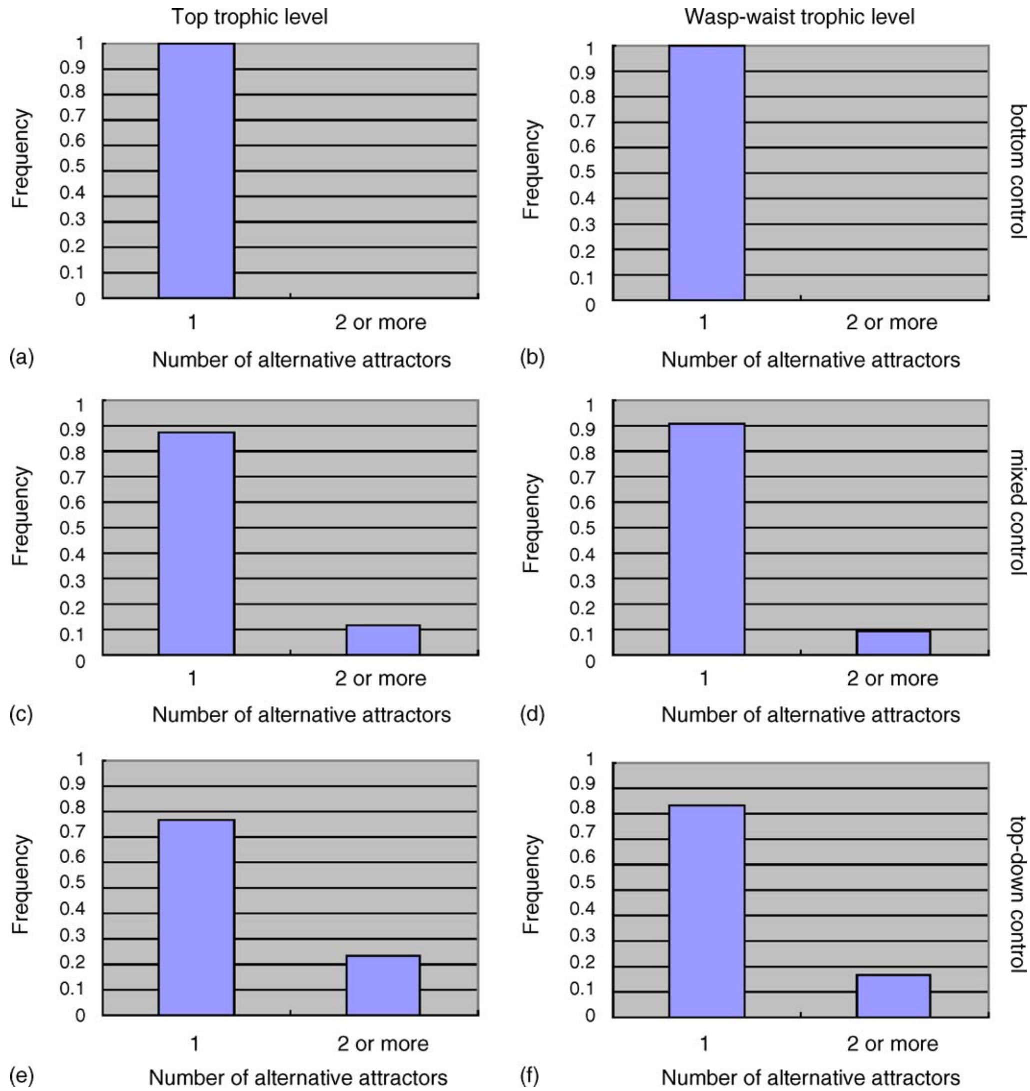

Fig. 3 – (a–f) Relative frequency of the number of attractors in marine ecosystems.

For the condition that the control mechanism is mixed, there are alternative attractors in the studied marine models. When the fishing object is top trophic level, alternative attractors exist in 5 models (13.9%) among the 36 experiments (*Antractica*, *Weddell Sea*; *Canada*, *Eastern Scotian Shelf—1990s*; *Canada*, *Grand Banks of Newfoundland—1900s*; *Iceland—1950*; *South Africa*, *Northern Benguela—1990s*). When the fishing group is intermediate trophic level, alternative attractors exist in four models (11.4%) (*Antractica*, *Weddell Sea*; *Canada*, *Grand Banks of Newfoundland—1980s SH*; *Canada*, *Grand Banks of Newfoundland—1990s*; *USA*, *Alaska*, *Prince William Sound*; see Table 2).

When the control mechanism is top-down and the fishing object is top trophic level, eight (22.8%) models found evidence for the alternative attractors (*Antractica*, *Weddell Sea*; *Australia*, *South East Shelf*; *Canada*, *Eastern Scotian Shelf—1990s*; *Canada*, *Grand Banks of Newfoundland—1900s*; *China*, *Bohai Sea*; *Iceland—1950*; *South Africa*, *Northern Benguela—1990s*; *USA*, *Alaska*, *Prince William Sound*). When the fishing object intermediate trophic level, six (16.7%) models found evidence for the alternative attractors (*Antractica*, *Weddell Sea*; *Australia*, *South East Shelf*; *Canada*, *Grand Banks of Newfoundland—1980s SH*; *Canada*, *Grand Banks of Newfoundland—1990s*; *French Polynesia*, *Moorea Fringing Reef*; *USA*, *Alaska*, *Prince William Sound*; see Table 2).

4. Discussion

4.1. *Existence of alternative attractors in marine ecosystems*

The presence of alternative attractors has profound implications for ecosystem management as it may imply catastrophic collapse of the system and large restoration efforts (Scheffer et al., 2001). However, manipulating marine ecosystems to demonstrate the existence of alternative attractors is very difficult (Collie et al., 2004). This paper presents a new approach to detect the different stable states in system with the software *EwE*. The results (see Fig. 3 and Table 2) show that there are

Table 2 – The existence of alternative attractors for each of two test cases (top and inter) under each of the flow control type: top-down, mixed and bottom-up

Marine ecosystem	Bottom-up		Mixed		Top-down	
	Top	Inter	Top	Inter	Top	Inter
Weddell Sea	1P[a]	1P	P–C[b]	P–C	P–C	P–C
Darwin Harbour	1P	1P	1P	1P	1P	1P
South East Shelf	1P	1P	1P	1P	P–C	P–C
Bight coastal ecosystem	1P	1P	1P	1P	1P	1P
Caete mangrove estuary	1P	1P	1P	1P	1P	1P
Eastern Scotian Shelf—1980s	1P	1P	1P	1P	1P	1P
Eastern Scotian Shelf—1960s	1P	1P	2P[c]	1P	2P	1P
Grand Banks of Newfoundland—1900s	1P	1P	2P	1P	2P	1P
Grand Banks of Newfoundland—1980s AB	1P	1P	1P	1P	1P	1P
Grand Banks of Newfoundland—1980s SH	1P	1P	1P	2P	1P	2P
Grand Banks of Newfoundland—1990s	1P	1P	1P	2P	1P	2P
Northern Gulf of St. Lawrence—1980s	1P	1P	1P	1P	1P	1P
Southern Gulf of St. Lawrence—1980s	1P	1P	1P	1P	1P	1P
Bohai Sea	1P	1P	1P	1P	2P	1P
Faroe Islands—1997	1P	1P	1P	1P	1P	1P
Bay of Biscay—1998	1P	1P	1P	1P	1P	1P
Moorea Fringing Reef	1P	1P	1P	1P	1P	P–C
Floreana rocky reef	1P	1P	1P	1P	1P	1P
Guinea—1998	1P	1P	1P	1P	1P	1P
Iceland—1950	1P	1P	2P	1P	2P	1P
Iceland—1997	1P	1P	1P	1P	1P	1P
Mauritania EEZ—1987	1P	1P	1P	1P	1P	1P
Mauritania EEZ—1998	1P	1P	1P	1P	1P	1P
Tamiahua Lagoon	1P	1P	1P	1P	1P	1P
Laguna de Bay—1968	1P	1P	1P	1P	1P	1P
Laguna de Bay—1980	1P	1P	1P	1P	1P	1P
San Miguel Bay	1P	1P	1P	1P	1P	1P
Azores—1997	1P	1P	1P	1P	1P	1P
Northern Benguela—1970s	1P	1P	1P	1P	1P	1P
Northern Benguela—1980s	1P	1P	1P	1P	1P	1P
Northern Benguela—1990s	1P	1P	2P	1P	2P	1P
Chiku lagoon	1P	1P	1P	1P	1P	1P
Prince William Sound	1P	1P	1P	2P	2P	P–C
Prince William Sound (Old)	1P	1P	1P	1P	1P	1P
USA, Mid Atlantic Bight	1P	1P	1P	1P	1P	1P
West Florida Shelf	1P	1P	1P	1P	1P	1P

[a] 1P: one point attractor.
[b] P–C: one point attractor and one cyclic attractor.
[c] 2P: two point attractors.

indeed alternative attractors in some of the studied marine ecosystems based the criteria for diagnosing discontinuous regime shift, and the flow control mechanism and trophic level have great effect on the existence of the alternative attractors. We will discuss these effects in following sections.

4.2. *Effect of the control mechanism*

The results in this paper (Fig. 3) suggested that the control mechanism could affect the ecosystem dynamics that would alter the structure and function of the studied marine ecosystem greatly. When the control mechanism is bottom-up, there is only one stable state (1P) of the system; when the control mechanism is mixed, there are five (top trophic level) and four (inter trophic level) models which have alternative attractors, respectively. Finally, when the top-down control mechanism is studied, the results show there are more models with alternative attractors (eight for top trophic level and six for inter trophic level). Identification of the interaction among the ecosystem may have deep implication to the protection, restoration and good understanding on succession of the system, and it is important to identify the control mechanism of the ecosystem in detecting alternative attractors.

4.3. *Effect of the trophic level*

When the fishing trophic level changed from top to intermediate, the occurrence frequency of the alternative attractors changed slightly, but the models with alternative attractors changed significantly. When the control mechanism is mixed and the fishing trophic level changed from top to wasp-waist, the number of models with alternative attractors changed from five to four. Among these models with alternative attractors, only one system (*Antractica*, *Weddell Sea*) unchanged. When the control mechanism is top-down and the fishing trophic level changed from top to wasp-waist, the number of models with alternative attractors changed from eight to six. Among these models with alternative attractors, there are only two models (*Antractica*, *Weddell Sea* and *South East Shelf*) unchanged.

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