

# Evaluating Network Analysis Indicators of Ecosystem Status in the Gulf of Alaska

Johanna Jacomina Heymans,<sup>1,\*</sup> Sylvie Gu enette,<sup>2</sup> and Villy Christensen<sup>2</sup>

<sup>1</sup>Scottish Association for Marine Science, Dunstaffnage Marine Laboratory, Dunbeg, Oban PA 37 1QA, Scotland; <sup>2</sup>University of British Columbia, Fisheries Centre, 2202 Main Mall, V6T 1Z4 Vancouver, British Columbia, Canada

## ABSTRACT

This is the first study on the emergent properties for empirical ecosystem models that have been validated by time series information. Ecosystem models of the western and central Aleutian Islands and Southeast Alaska were used to examine indices of ecosystem status generated from network analysis and incorporated into Ecopath with Ecosim. Dynamic simulations of the two ecosystems over the past 40 years were employed to examine if these indices reflect the dissimilar changes that occurred in the ecosystems. The results showed that the total systems throughput (TST) and ascendancy (*A*) followed the climate change signature (Pacific decadal oscillation, PDO) in both ecosystems, whereas the redundancy (*R*) followed the inverse trend. The different trajectories for important species such as Steller sea lions (*Eumetopias jubatus*), Atka mackerel (*Pleurogrammus monopterygius*), pollock (*Theragra chalcogramma*), herring (*Clupea pallasii*), Pacific cod (*Gadus macro-*

*cephalus*) and halibut (*Hippoglossus stenolepis*) were noticeable in the Finn cycling index (FCI), entropy (*H*) and average mutual information (AMI): not showing large change during the time that the Stellers sea lions, herring, Pacific cod, halibut and arrowtooth flounder (*Atheresthes stomias*) increased in Southeast Alaska, but showing large declines during the decline of Steller sea lions, sharks, Atka mackerel and arrowtooth flounder in the Aleutians. On the whole, there was a change in the emergent properties of the Aleutians around 1976 that was not seen in Southeast Alaska. Conversely, the emergent properties of both systems showed a change around 1988, which indicated that both systems were unstable after 1988.

**Key words:** Gulf of Alaska; Ecopath with Ecosim; network analysis; ecosystem indicators; redundancy; ascendancy.

## INTRODUCTION

Network analysis consists of a suite of algorithms (Ulanowicz 1986; Ulanowicz and Kay 1991; Ulanowicz and Norden 1990; Ulanowicz and Puccia 1990) incorporated into Ecopath by Christensen and Pauly (1992) and lately into Ecosim (Christensen and others 2005). It incorporates analytical

techniques for studying indirect trophic effects and the structure of recycling pathways by assessing overall ecosystem characteristics as a set of mathematical measures to quantify its organization and redundancy (Ulanowicz and Kay 1991). Various network analysis indices have been used as indicators of ecosystem stability and stress, including the Finn cycling index (FCI) (Vasconcellos and others 1997), ascendancy (Ulanowicz 2001), redundancy or internal flow overhead (Heymans and others 2002), entropy and average mutual

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\*Corresponding author; e-mail: sheilaheyman@yahoo.com

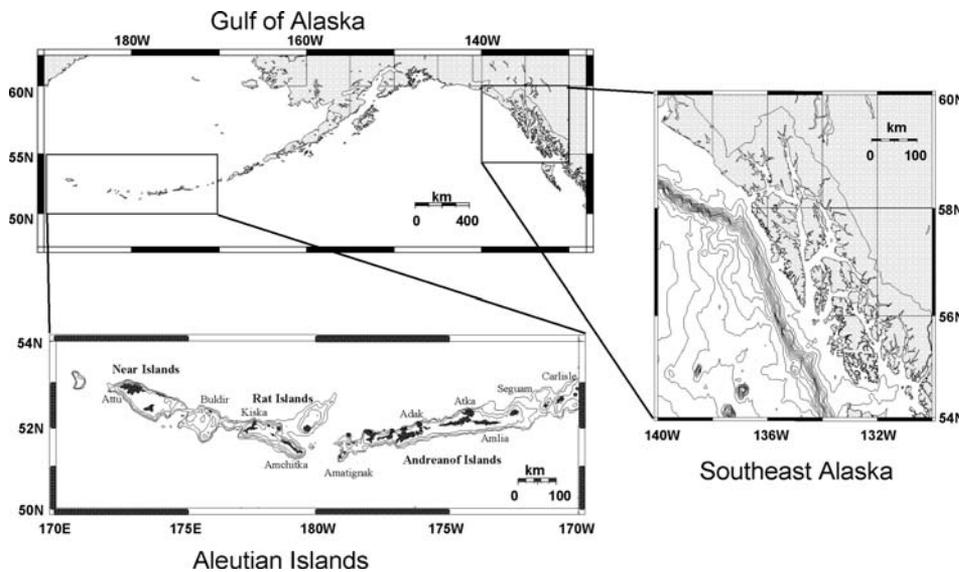


Figure 1. A map of the North Pacific showing the two model areas in the Gulf of Alaska, namely the western and central Aleutian Islands (Aleutian Islands), and Southeast Alaska. Maps created from the OMC website at [http://www.aquarius.geomar.de/omc/make\\_map.html](http://www.aquarius.geomar.de/omc/make_map.html).

information (AMI) (Mageau and others 1998). These indices have only been calculated for static ecosystem models and compared among systems or between different time periods for the same system, but have thus far not been studied using dynamic simulations.

According to Proulx and others (2005) “network studies in biology have reached a turning point, where empirical studies must provide the motivating details for novel theory, and theoretical studies must provide a rigorous predictive framework in which to test hypotheses about network formation and network function”. To this end, this paper used empirical data and Ecopath models of two ecosystems in the Gulf of Alaska to provide a predictive framework for the effects of climate change and fishing on these two ecosystems. Proulx and others (2005) also suggested that we need to use models that reflect biological reality to effectively test hypotheses about network structure. Thus, the two Ecopath models that were built for the year 1963 were simulated forward using Ecosim and known catch rates, subjected to environmental change as encompassed by the Pacific Decadal Oscillation (PDO) and validated by time series catch and biomass data in Heymans and others (2005). The two ecosystems represented here had very different systems trajectories due to differences in fishing and climate. The hypothesis is that these differences in ecosystem trajectories should be discernable in their emergent network analysis indices. A corollary to this hypothesis is that the two systems reacted differently to the environmental variation that they were subjected to, and this should also be seen in the emergent properties of the system.

## Study Site

Two ecosystems in the Gulf of Alaska were compared for this study: the central and western Aleutian Islands (henceforth Aleutian Islands) and Southeast Alaska. The Aleutian Island chain is 1,770 km long (Figure 1) and stretches from the Alaskan Peninsula to close to Siberia (Murie 1959). However, the Aleutian Island area used in this study stretches from 170°W to 170°E around the islands, to the 500 m depth contour, for an area of approximately 57,000 km<sup>2</sup> (Heymans 2005). The model for Southeast Alaska comprised the shelf east of 140°W to 1,000 m depth, although most of the study area (89%) is shallower than 300 m (Gu nette 2005). The model encompasses the eastern part of the Yakutat region (140–137°W) and southeast Alaska east of 137°W, for a study area of approximately 91,000 km<sup>2</sup> (Gu nette 2005).

## MATERIALS AND METHODS

Ecopath with Ecosim (EwE) models were constructed of the Aleutian Islands and Southeast Alaska ecosystems representing 1963, the start of the major fisheries. The models were driven by catch rates and fitted to time series data of catch and biomass over 40 years. The Southeast Alaska model was documented by Gu nette (2005) and the Aleutian Islands by Heymans (2005). Both models consisted of 40 compartments and were structurally similar.

The models were subjected to environmental variation using the PDO index to drive the Southeast Alaska model and the inverse of the PDO

(-PDO) to drive the Aleutian Islands. The PDO tracks the geographic pattern of sea surface temperature (SST) anomalies in the North Pacific Ocean and reflects the pattern of central ocean SST anomalies (Welch and others 2000). The effect of the PDO is therefore opposite in the Aleutians to that in Southeast Alaska, as the SST anomalies are different in the two areas (Heymans and others 2005). This was also confirmed by the finding that the Aleutians the PDO was negatively correlated in the primary production anomaly obtained from the data, whereas in Southeast Alaska the correlation was positive (Heymans and others 2005).

Ecosim estimated goodness-of-fit measures to measure the variance between the predicted and observed parameters of biomass and catch: the goodness-of-fit measure is a weighted sum of squares (SS) deviation of log biomasses from log predicted biomasses (Christensen and Walters 2004). This goodness-of-fit measure showed that the inverse trajectory should be used as the effect of the PDO is negative in the Aleutians and positive in Southeast Alaska (Heymans and others 2005). The PDO and -PDO indices had to be rescaled with an average of one and a range of two to drive the models, and these indices and their 5 year running average are given in Figure 2. In addition, the SST on which the PDO was based has shown at least two directional changes over the past 40 years. The highest value of the 5 year running average of the PDO was in March 1988, whereas the lowest value was in January 1976 (see dashed lines in Figure 2). These turning points have been linked to regime shifts in the Gulf of Alaska, although not in the Aleutian Islands or Southeast Alaska (Anderson and Piatt 1999; Hare and Mantua 2000). The simulated best fit trajectories of both models were subjected to network analysis and the results compared.

## The EwE Model

The Ecopath model is based on a system of linear equations for expressing mass-balance and the linear equation for an arbitrary period is:

$$B_{(i)} \cdot (P/B)_{(i)} \cdot EE_{(i)} = C_{(i)} + \sum_j \{B_{(j)} \cdot (Q/B)_{(j)} \cdot DC_{(ij)}\} + E_{(j)} + BA_{(i)} \quad (1)$$

where  $B_{(i)}$  is the biomass of component  $i$  during the period covered,  $(P/B)_{(i)}$  is the production of a component  $i$  per unit biomass of  $i$ ,  $EE_{(i)}$  is the ecotrophic efficiency (the fraction of the total production consumed by predators or exported from

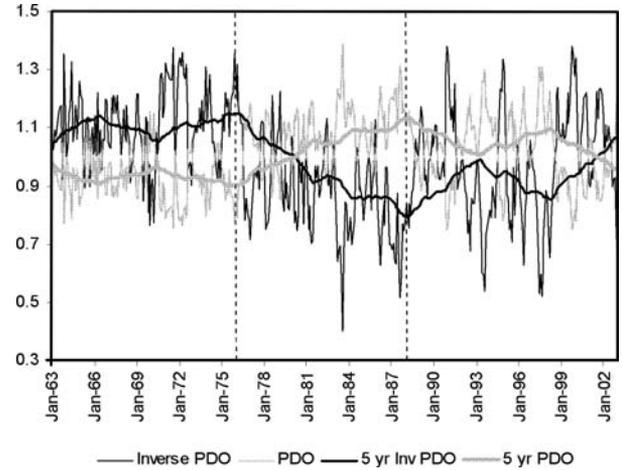


Figure 2. Pacific Decadal Oscillation index (PDO, grey), inverse PDO (black) and 5 year running average of both (thicker lines) used to drive the Southeast Alaska and Aleutian Islands models, respectively. Included are the January 1976 and March 1988 turning points in the 5 year running average values for the PDO and inverse PDO as used in this paper (dotted lines).

the system) of component  $i$ ,  $C_{(i)}$  is the catch of component  $i$ ,  $B_{(j)}$  is the biomass of each of the  $j$  predators of  $i$ ,  $(Q/B)_{(j)}$  is the consumption of component  $j$  per unit biomass,  $DC_{(ij)}$  is the average fraction of  $i$  in the diet of  $j$ , in terms of weight,  $E_{(i)}$  is the net migration rate of compartment  $i$  and  $BA_{(i)}$  is the biomass accumulation of compartment  $i$  (Christensen and Walters 2004).

Ecosim uses a set of differential equations to calculate the changes in biomass of each group over time, using the harvest rates as well as external forcing functions imposed on the ecosystem (Christensen and others 2000). The equations are derived from the Ecopath master equation (Eq. 1), and take the form

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (M0_i + F_i + e_i) B_i \quad (2)$$

where  $dB_i/dt$  represents the growth rate during the time interval  $t$  of group  $i$  in terms of its biomass  $B_i$ ,  $g_i$  is the net growth efficiency,  $M0_i$  the non-predation ("other") natural mortality rate,  $F_i$  is fishing mortality rate,  $e_i$  is emigration rate,  $I_i$  is immigration rate (assumed constant over time, and hence independent of events in the ecosystem modelled), and  $e_i \cdot B_i - I_i$  is the net migration rate (Christensen and Walters 2004). The two summations estimate consumption rates, the first calculating the total consumption by group  $i$ , and the second the predation by all predators  $i$  on the same group  $i$ . The

consumption rates  $Q_{ji}$  are calculated based on the “foraging arena” concept, where  $B_i$  values are divided into vulnerable and invulnerable components sensu Walters and others (1997). The transfer rate ( $v_{ij}$ ) between the vulnerable and invulnerable components determines if control is top-down (that is, Lotka–Volterra), bottom-up (that is, donor-driven), or of an intermediate type (Christensen and Walters 2004). Top-down versus bottom-up control is a continuum in the model, where low vulnerabilities imply bottom-up and high vulnerabilities top-down control. Consumption at each time step is calculated by:

$$Q_{ij} = \frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot S_{ij} \cdot M_{ij} / D_j}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + a_{ij} \cdot M_{ij} \cdot B_j \cdot S_{ij} \cdot T_j / D_j} \quad (3)$$

where  $a_{ij}$  is the rate of effective search for  $i$  by  $j$ ,  $T_i$  represents prey relative feeding time,  $T_j$  the predator relative feeding time,  $S_{ij}$  the user-defined seasonal or long-term forcing effects,  $M_{ij}$  the mediation forcing effects, and  $D_j$  represents effects of handling time as a limit to consumption rate. See Walters and others (1997), Walters and Kitchell (2001), Walters and others (2000) and Christensen and Walters (2004) for further information on these algorithms.

## The Network Analysis Indicators

The network analysis indicators used to examine the status of the two ecosystems as depicted by their Ecopath with Ecosim models include total systems throughput (TST in  $\text{t km}^{-2} \text{ year}^{-1}$ ), systems entropy ( $H$ ), AMI, ascendancy ( $A$ ), redundancy ( $R$  or overhead on internal flows) and FCI (%) (Heymans 2003). The unit for  $H$ , AMI,  $A$ , and  $R$  is “flowbits”, or the product of flow (for example,  $\text{t km}^{-2} \text{ year}^{-1}$ ) and bits and the bits is an information unit that corresponds to the amount of uncertainty associated with a single binary decision (Christensen and others 2005). TST is the sum of all flows in the model (Finn 1976),

$$\text{TST} = \sum_{i=1, j=1}^n T_{ij} \quad (4)$$

where  $T_{ij}$  is the flow between any two compartments and it includes all outflows (respiration, catch, export) from each compartment. The diversity of flows or systems entropy ( $H$ ) is an indication of the total uncertainty embodied in the given configuration of flows of the system and represents the total number and diversity of flows in a system (Mageau and others 1998), and is calculated by Ulanowicz (2004) as:

$$H = - \sum_{ij} \frac{T_{ij}}{\text{TST}} \cdot \log \left( \frac{T_{ij}}{\text{TST}} \right) \quad (5)$$

The AMI measures the organization of the exchanges among components. A rise in AMI signifies that the system is becoming more constrained and is channeling flows along more specific pathways (Ulanowicz and Abarca-Arenas 1997). The AMI is calculated as:

$$\text{AMI} = \sum_{ij} \left( \frac{T_{ij}}{\text{TST}} \right) \cdot \log \left( \frac{T_{ij} \cdot \text{TST}}{T_j \cdot T_i} \right) \quad (6)$$

where  $T_i$  is the sum of all material leaving the  $i$ th component and  $T_j$  is the sum of all flows entering the  $j$ th component (Ulanowicz 2004). Ascendancy describes both the growth (TST) and development (AMI) of the system (Ulanowicz 1986) and is the product of TST and AMI, and in Ecopath is defined in terms of flow, or:

$$A = \sum_{ij} (T_{ij}) \cdot \log \left( \frac{T_{ij} \cdot \text{TST}}{T_j \cdot T_i} \right) \quad (7)$$

In the results the ascendancy is given as percentage of the development capacity ( $C$ ) which is a product of TST and the entropy ( $H$ ), and is the upper limit to the ascendancy.

The complement to the ascendancy is the overhead, which gauges the inefficient degrees of freedom that a system retains (Ulanowicz 2000). Overhead is divided into export, dissipation and internal flow (Ulanowicz 2000), and the internal flow overhead (IFO or  $R$ ) seems to be the best indicator of a change in degrees of freedom of the system, that is, what is the distribution of energy flow among the pathways in the ecosystem. It is also defined as the pathway redundancy (Ulanowicz 1997). The redundancy is calculated as (Ulanowicz 2004):

$$R = - \sum_{i=1}^n \sum_{j=1}^n (T_{ij}) \cdot \log \left( \frac{T_{ij}^2}{\sum_{j=1}^n T_{ij} \cdot \sum_{i=1}^n T_{ij}} \right) \quad (8)$$

Similar to the ascendancy, it is here presented as a percentage of the development capacity. If the  $R$  is high, the flows among the pathways are not concentrated in one or two main pathways but there are many alternative pathways for energy to get from one compartment to another. Christensen (1995) linked the overhead to ecosystems stability and Heymans (2003) proposed  $R$  as an index of the system’s resilience. A trade-off develops between the increasing efficiency resulting from a network of exchanges dominated by only the most efficient

transfers, and the vulnerability resulting from the rigidity of such a flow configuration.

The FCI quantifies the relative amount of recycling and is an indication of stress and structural differences either among models (Finn 1976) or through time, and is calculated as:

$$\text{FCI} = \frac{\text{TST}_c}{\text{TST}} \quad (9)$$

where  $\text{TST}_c$  is the total flow that is recycled, and TST is the total flow through the system as calculated in Eq. 4.

## RESULTS

The biomass series from fitted Ecosim runs for some of the important species in both the Aleutian Islands and Southeast Alaska are given in Figure 3A and B, respectively. These fits were obtained by fitting the models to the time series data as shown in Figure 3. The effects of environmental variation were included using the PDO and -PDO as drivers on the primary production (phytoplankton) of the Southeast Alaska and Aleutian Islands models, respectively. The methods and results for fitting these models to environmental and time series data are given in Heymans and others (2005) with special reference to fitting for the Steller sea lions (*Eumetopias jubatus*) in Gu enette and others (2006).

The TST, entropy ( $H$ ), ascendancy ( $A$ ), AMI, FCI, and redundancy ( $R$ ) were extracted from the best fitted runs of the two models on a monthly time-step and plotted against time. The cumulative averages of these indices were calculated for the first 5 years and thereafter the 5 year running averages were calculated as well as the absolute percentage difference between the monthly index and the running average. In addition, the average of the absolute percentage difference between the monthly indices and the running average were calculated for the 1963–1976, 1977–1988 and 1989–2001 time periods, as 1976 and 1988 stood out at the turning points in the climate change variables (Figure 2).

The monthly time-step TST and the 5 year running average TST for the Aleutians and Southeast Alaska are shown in Figure 4A, whereas the absolute percentage difference between the monthly TST and running average TST is given in Figure 4B. The TST is mainly driven by the flow through phytoplankton, zooplankton, invertebrates and other groups with large flows, and therefore the effects of fishing and the changes seen in Figure 3 did not affect the TST trajectory much. The TST in the two systems both started off around

5,000 t km<sup>-2</sup> year<sup>-1</sup>, but fluctuated in different directions with the minimum TST in the Aleutians being in July 1983 at approximately 3,500 t km<sup>-2</sup> year<sup>-1</sup> and the maximum in March 1972 at approximately 5,800 t km<sup>-2</sup> year<sup>-1</sup>, when Southeast Alaska had its minimum TST (~4,200 t km<sup>-2</sup> year<sup>-1</sup>). However, the maximum TST in Southeast Alaska was not in July 1983, when the Aleutians had its minimum, but in September 1987 (~6,400 t km<sup>-2</sup> year<sup>-1</sup>), which indicates that the PDO and -PDO did not have precisely the same effect on both ecosystems.

The percentage difference between the cumulative average and the monthly TST, however, seems to be very similar in the two systems (Figure 4B) and the TST seems to follow the PDO and -PDO trajectories in Southeast Alaska and the Aleutian Islands, respectively. Finn (1976) suggested that growth or decline of the TST could be a sensitive indicator of the state of the system, specifically if the number of compartments stays the same, and this is evident in the Aleutians where the flow through the system declined after 1976 while the flow through Southeast Alaska system increased at the same time. The general reduction in biomass for species in the Aleutians (Figure 3A), specifically for Steller sea lions, sharks and skates (mostly *Lamna ditropis*, *Squalus acanthias*, *Raja binoculata*), Atka mackerel (*Pleurogrammus monopterygius*), pollock (*Theragra chalcogramma*) and Pacific Ocean perch (*Sebastes alutus*) probably caused the decline in the flows in that system, whereas there was an increasing trend in the biomass for many species in Southeast Alaska during the same time (Figure 3B), which would increase the TST.

The monthly time step of systems entropy ( $H$ ) showed that although the PDO had relatively similar effects on the two systems, in terms of TST (or growth), its effect on the diversity of flows within the systems was very different (Figure 5A). The entropy in both systems started off at around 3.2 but it declined substantially in the Aleutians after 1976, while staying relatively constant in Southeast Alaska. In addition, the absolute percentage difference between the monthly calculation and the average entropy (Figure 5B) was much higher in the Aleutians than in Southeast Alaska and the percentage difference is less than in the TST (Figure 4B). The reduction in biomass of important species in the Aleutians, for example, the Steller sea lions, sharks and skates, Atka mackerel and pollock after 1976 would reduce the uncertainty in the flow configuration, as a reduced biomass pool would reduce the number of flows possible through that pool and the possible path-

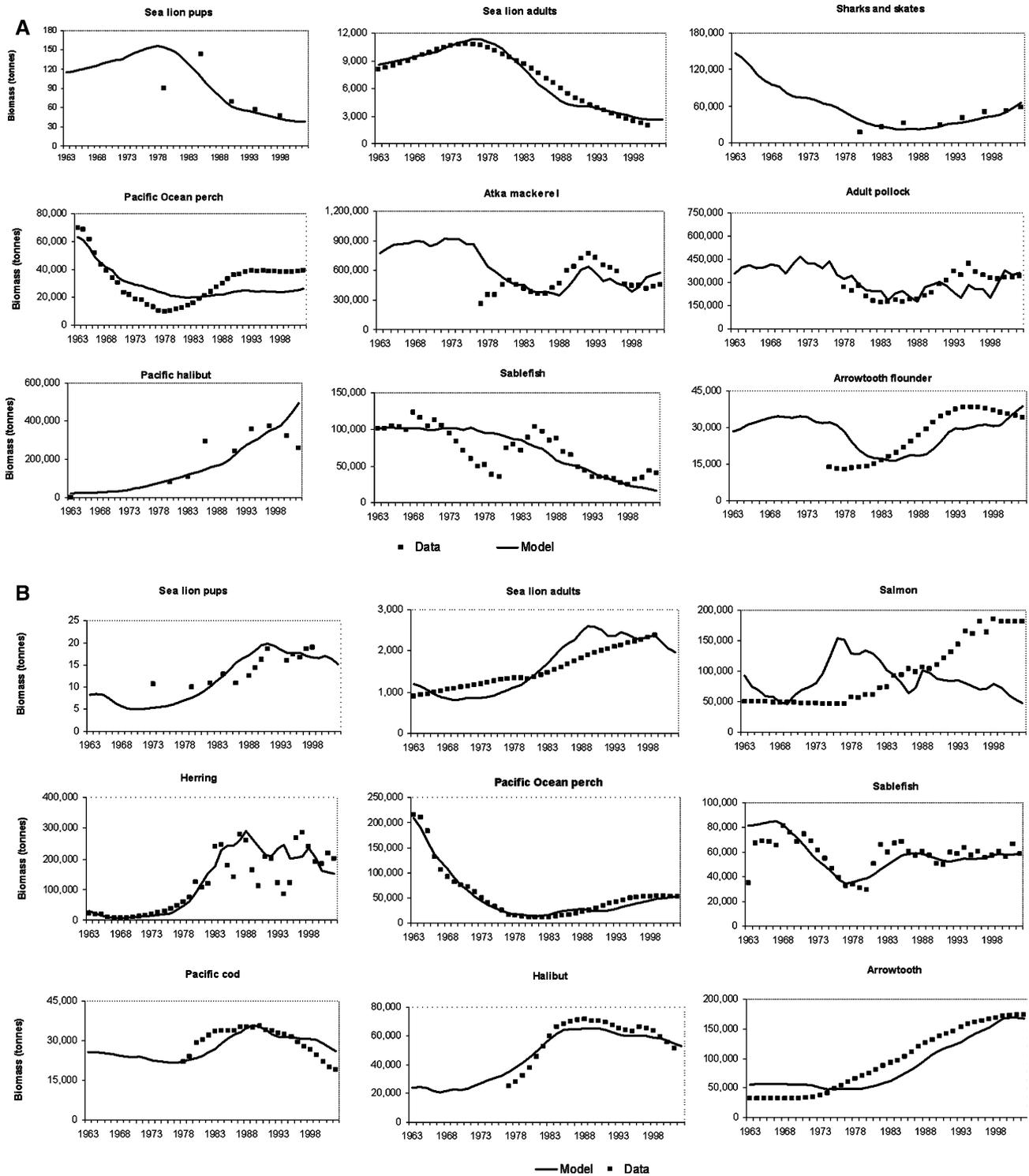


Figure 3. Biomass (tonnes) and model predictions of the Aleutian Islands (A) and Southeast Alaska (B) models after fitting the models to the data.

ways a particle of mass or energy could take. In contrast, in Southeast Alaska, the reduction in Pacific Ocean perch and sablefish (*Anoplopoma fimbria*) was negated by the increase in top predators

such as Steller sea lions, an increase in secondary predators such as halibut and arrowtooth flounder and an increase in the important prey species (herring, *Clupea pallasii*). The decrease in some

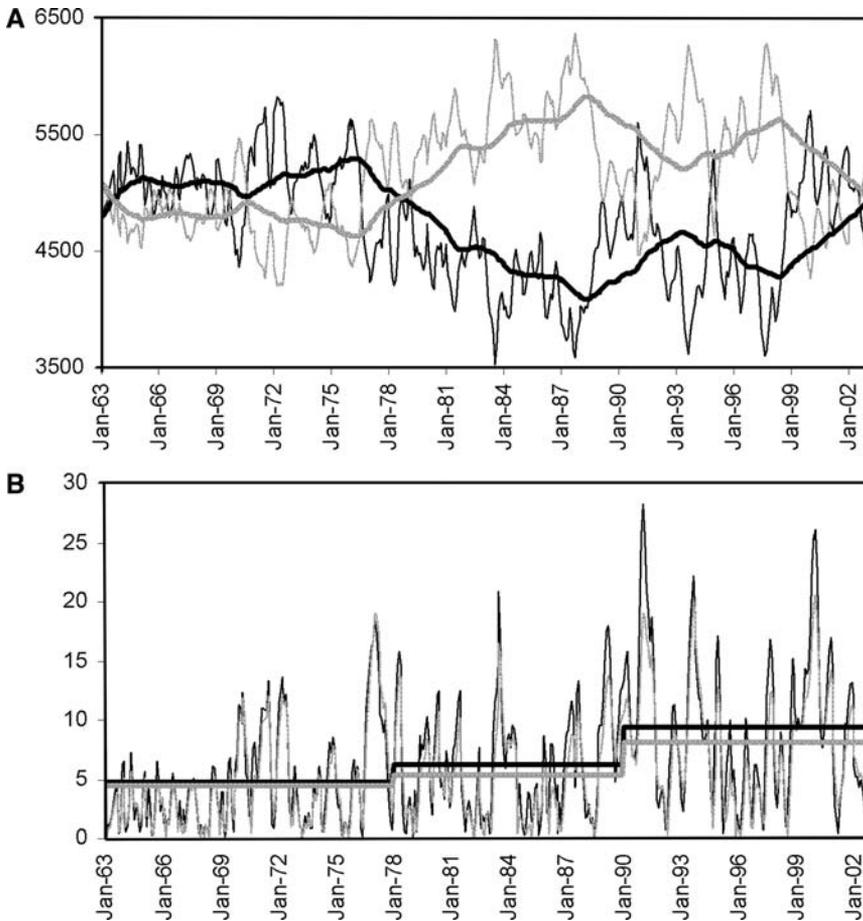


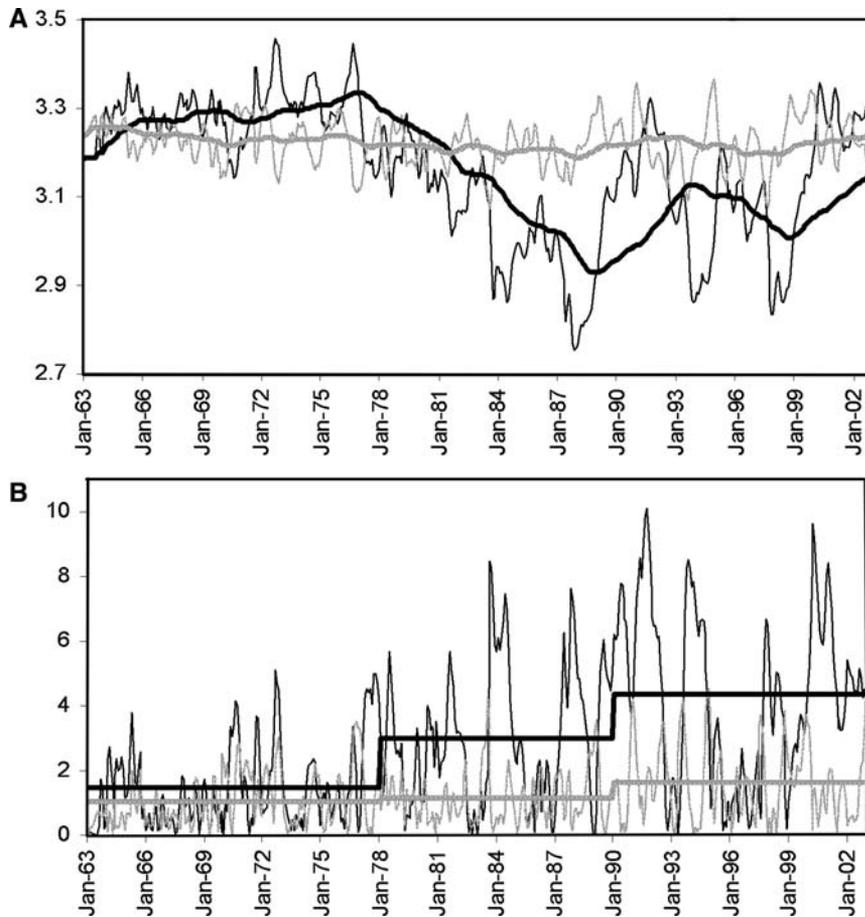
Figure 4. Changes in the total systems throughput (TST). **A** TST in Southeast Alaska (grey) and Aleutian Islands (black) and the 5 year running averages of those values in both systems (thicker lines). **B** The absolute percentage difference between the monthly TST and 5 year running average TST for the Aleutians (black) and Southeast Alaska (grey). Straight lines indicate the average percentage difference pre- and post-1976 and 1988.

parts of the ecosystem was therefore negated by an increase somewhere else, which kept the uncertainty of the given configuration of flow paths relatively constant.

In contrast to the TST and *H*, the ascendancy of the two systems was very different from the first month with the Aleutians having a much higher ascendancy, around 70% compared to the approximately 27% for Southeast Alaska (Figure 6A). Note that in Figure 6 the ascendancy is given as a percentage of the development capacity, and in the Aleutian Islands it fluctuated between 53% in July 1983 and 79% in December 1994, whereas in Southeast Alaska the range is five times less; between 25% in November 1972 and 30% in October 1998. The larger ascendancy in the Aleutians indicates that the system is channeling more large flows through a few important pathways. Specifically, with the large decline in Steller sea lions in the Aleutians after 1979 and the decline in Atka mackerel and pollock (some of the main prey species for sea lions) after 1990 (Figure 3A), the energy could not flow through those usual pathways to the top predators thus channeling flows

through fewer pathways and therefore increasing the ascendancy. Similarly, the decline in sablefish in the late 1970s in Southeast Alaska (Figure 3B) could explain the spike in ascendancy in that system at that time, although it did not seem to have such a lasting impact as in the Aleutians. Nevertheless, the ascendancy for the Aleutians and Southeast Alaska still show similar trends to the TST as it fluctuates with the  $-PDO$  and  $PDO$ , respectively (Figure 6A) because the fluctuations in ascendancy are probably due to fluctuations in throughput (Figure 4A) and not information. However, the absolute difference between the monthly ascendancy and the 5 year running average was again much smaller in Southeast Alaska than in the Aleutians, especially after 1977, although the percentage difference was higher in general than for the entropy (Figure 6B).

The AMI (Figure 7A), showed a similar trend to the systems entropy in that the running average follows the  $-PDO$  in the Aleutians but it does not follow the  $PDO$  for Southeast Alaska. Similarly, the percentage difference is higher in the Aleutians than in Southeast Alaska, and the variation is

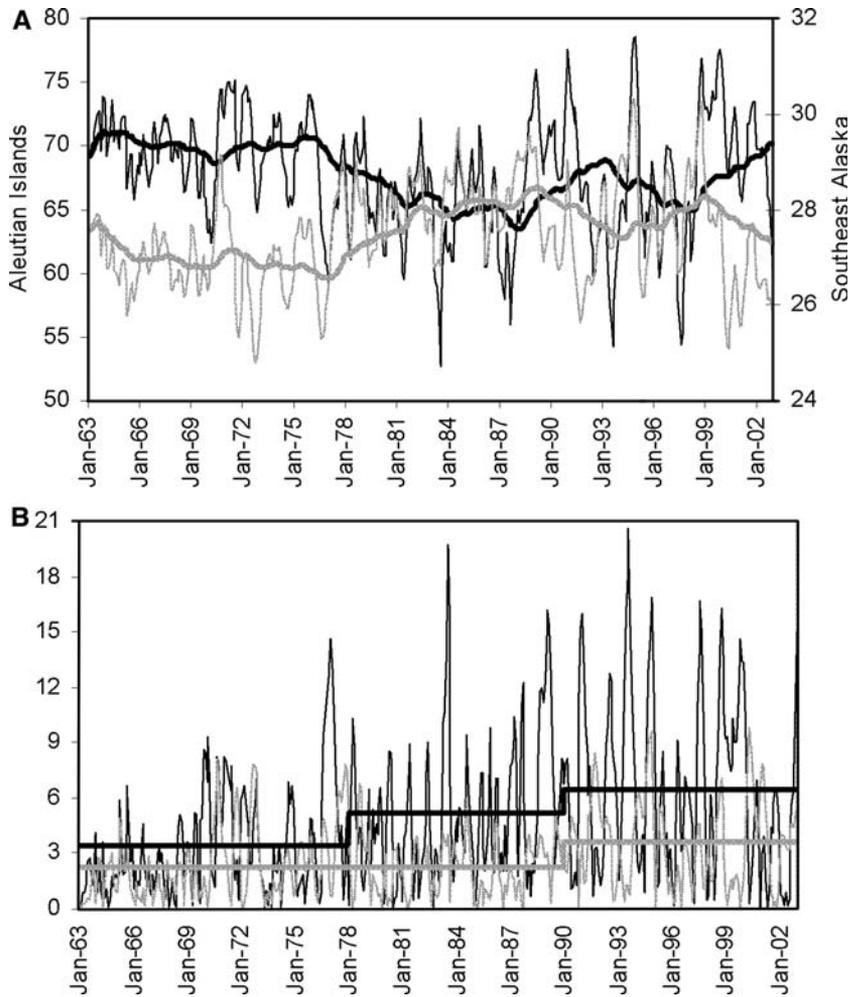


**Figure 5.** Changes in the entropy ( $H$ ). **A** Entropy in Southeast Alaska (grey) and Aleutian Islands (black) and the 5 year running averages of those values in both systems (thicker lines). **B** The absolute percentage difference between the monthly entropy and running average entropy for the Aleutians (black) and Southeast Alaska (grey). Straight lines indicate the average percentage difference pre- and post-1976 and 1988.

much higher (maximum value  $>20\%$ , Figure 7B) than that of the entropy (maximum value  $\sim 10\%$  Figure 5B). The AMI quantifies the degree of constraint or organization in the system (Ulanowicz 2000), and we see that even though the Aleutians were more constrained than Southeast Alaska, with the flows well organized through fewer pathways, the system became less constrained after 1976, with a large decline in the constraint of the system in March 1977 (Figure 7A). The substantial reduction in Atka mackerel, Steller sea lions and sharks and skates around that time (Figure 3A) probably caused a change in the flow structure as it freed up energy to flow to various other predators, such as arrowtooth flounder and halibut. In contrast, in Southeast Alaska, no such large reduction in top predators was seen (Figure 3B), and consequently the AMI stayed very constant over time, and the flows were more complex in that system (Figure 7A). According to Latham and Scully (2002) “food webs buffer the effects of perturbation, while food chains, probably exhibiting an elevated AMI over web structures, were sensitive to network changes”, thus the higher AMI seen in the

Aleutians prior to 1976 indicates that the system was not as web-like as that of Southeast Alaska, and therefore the AMI declined after the important top predators and their prey declined. It is also obvious that there was an increase in the variation of the AMI in the Aleutians after 1977 (Figure 7B), whereas the AMI in Southeast Alaska did not vary substantially until after 1988.

As expected the redundancy (Figure 8A, B) of the Aleutians Islands was lower than that of Southeast Alaska, starting at approximately 34% in the Aleutians versus approximately 46% in Southeast Alaska. The higher redundancy in Southeast Alaska indicates that the system had more “strength in reserve” than the Aleutian Islands, which was reduced after 1976, whereas there was an increase in the redundancy of the Aleutians at that time. The redundancy showed an inverse trend to the primary production anomaly (PDO index) that drove these systems. Particularly, when the PDO was low at first and then increased over time, its effect on the redundancy of the Southeast Alaska system was high at first and then reduced over time. Similarly, in the Aleutians the



**Figure 6.** Changes in the ascendancy (A). **A** Ascendancy in Southeast Alaska (grey) and Aleutian Islands (black) and the 5 year running averages of those values in both systems (thicker lines). **B** The absolute percentage difference between the monthly ascendancy and running average ascendancy for the Aleutians (black) and Southeast Alaska (grey). Straight lines indicate the average percentage difference pre- and post-1976 and 1988.

–PDO was high in the first 15 years and reduced in the last 25 years, although its effect on the redundancy of the system was low and then high. Thus the inefficient degrees of freedom in the Aleutians were increased after the decline in Steller sea lions, Atka mackerel and pollock and the distribution of energy among the pathways was dispersed, whereas the inefficiency in Southeast Alaska declined when Steller sea lions, halibut and arrowtooth flounders started increasing and the energy was flowing along fewer pathways with more efficiency (Figure 3). However, the absolute percentage difference between the monthly redundancy and the running average was very similar between the two systems, with the Southeast Alaska system showing more fluctuations prior to 1976 and after 1988 (Figure 8B). Overall, the redundancy of the Aleutians did not seem to fluctuate as much as the ascendancy, with approximately 5% fluctuation in redundancy, whereas the ascendancy fluctuated by approximately 25%. The

reason for this difference is that redundancy is only a third of the complement to the ascendancy (the overhead) with export and dissipation also being important. Thus, some of the changes in ascendancy are reflected in the export and dissipation overhead instead of the redundancy, which means that the redundancy could be a less capricious index than ascendancy.

The FCI showed similar trends to the AMI and entropy as it followed the –PDO in the Aleutian Islands, but did not follow the PDO in Southeast Alaska (Figure 9A). Specifically, the decline in the TST after 1976 in the Aleutians is also seen as a decrease in recycling (FCI). Thus in the Aleutians after 1976, the decline in specifically sharks and skates and arrowtooth flounder, but also Steller sea lions, Atka mackerel, pollock and Pacific Ocean perch, decreased the recycling as well as the TST. Sharks and skates, as well as arrowtooth flounder and Pacific halibut all feed on detritus and discarded fish (Heymans 2005), and a reduction in

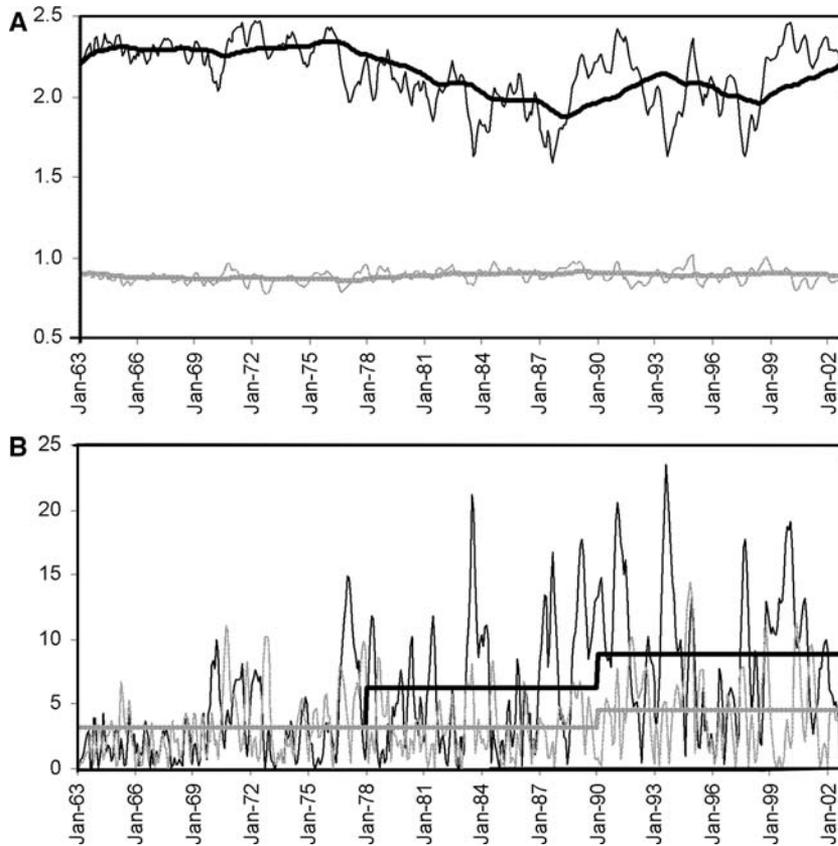
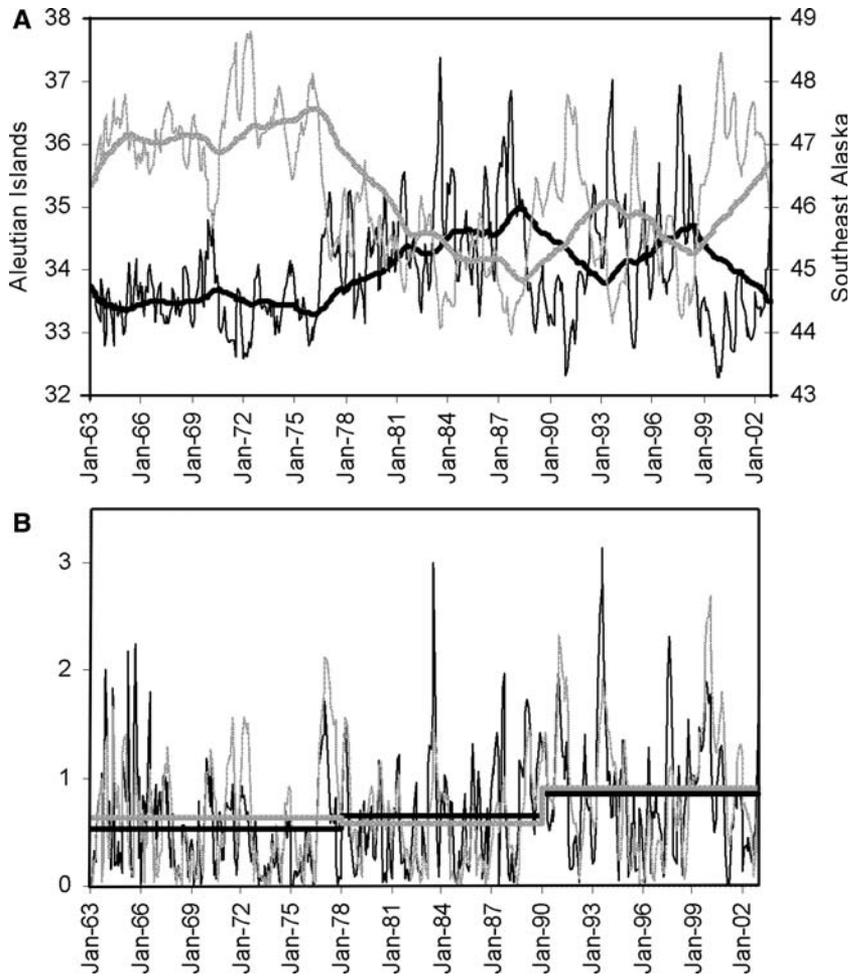


Figure 7. Changes in the average mutual information (AMI). **A** AMI in Southeast Alaska (grey) and Aleutian Islands (black) and the 5 year running averages of those values in both systems (thicker lines). **B** The absolute percentage difference between the monthly AMI and running average AMI for the Aleutians (black) and Southeast Alaska (grey). Straight lines indicate the average percentage difference pre- and post-1976 and 1988.

their numbers would decrease the recycling in the system. In addition the increase in FCI after the 1980s was probably due to the increase in sharks and skates, arrowtooth flounder and halibut increasing the recycling. In Southeast Alaska, on the other hand, the increase in TST was probably caused by the increase in Steller sea lions, herring, Pacific cod and halibut and did not lead to an increase in recycling, maybe because of the decline in Pacific Ocean perch, salmon (*Onchorhynchus gorbuscha*, *O. kisutch*, *O. Keta*, *O. tshawytscha* and *O. nerka*) and sablefish at the same time. Specifically, sablefish in Southeast Alaska (Gu nette 2005) was found to consume detritus (or discards) although this was not the case in the Aleutians, because the sablefish were mostly of smaller age classes and not adults; so they feed predominantly on invertebrates, cephalopods and zooplankton (Heymans 2005) whereas in Southeast Alaska they were more piscivorous (Gu nette 2005). Moreover, recycling in the Aleutians (FCI  $\sim$  1–3.5%) seems to be more important than in Southeast Alaska ( $\sim$ 0.6–1.2%), with the 5-year running average in Southeast Alaska hardly ever going above that of the Aleutians. Correspondingly, similar to most of the indices except the TST and *R*, the percentage dif-

ference between the monthly FCI and the running average was smaller in Southeast Alaska, whereas it shows large fluctuations in the Aleutian Islands (Figure 9B), specifically between 1976 and 1988. The fluctuations were more pronounced in Southeast Alaska prior to 1976 and after 1988 showing more stability in the recycling during the middle period.

One of the most interesting observations from these results is how the indices fluctuated pre- and post-climate change events. In Southeast Alaska the ascendancy (Figure 10B), and AMI (Figure 10D) showed no change in the intensity of their fluctuations after 1976, whereas the redundancy and entropy showed very little fluctuation (Figure 10D). Thus, in Southeast Alaska, most of the fluctuation in indices occurred after 1988. In contrast, for the Aleutian Islands, both events caused large variations, with the FCI (Figure 10C) fluctuating most between 1976 and 1988, and the TST (Figure 10A) most after 1988. In addition, the redundancy and FCI of Southeast Alaska have fluctuated less between 1976 and 1998, and most after 1988, suggesting that 1988 was more important in the Southeast Alaska system and 1976 was more important in the Aleutians.



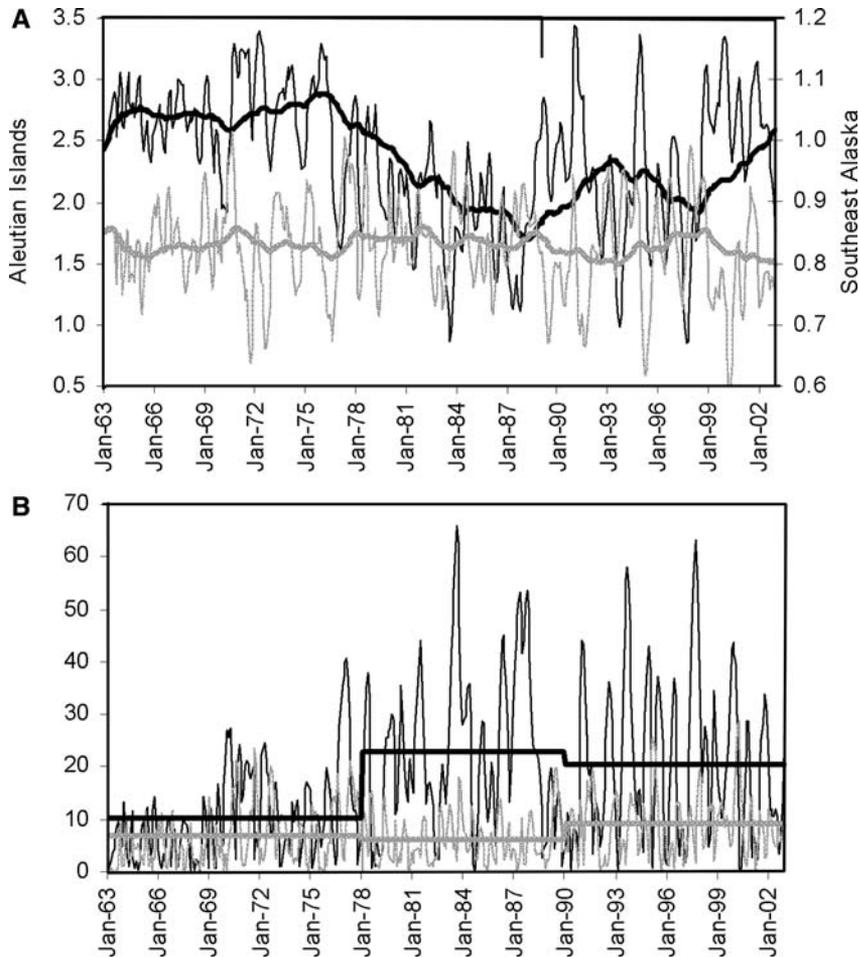
**Figure 8.** Changes in the redundancy ( $R$ ). **A** Redundancy in Southeast Alaska (grey) and Aleutian Islands (black) and the 5 year running averages of those values in both systems (thicker lines). **B** The absolute percentage difference between the monthly redundancy and running average redundancy for the Aleutians (black) and Southeast Alaska (grey). Straight lines indicate the average percentage difference pre- and post-1976 and 1988.

## DISCUSSION

Proulx and others (2005) said that they hoped that “network approaches will free us from the Gordian knot of accumulated data to reveal the global patterns behind large-scale ecological and evolutionary processes”. This is achieved here using a dynamic examination of the emergent properties of two ecosystems that have been influenced differently by climate change and fishing. This is the first study of emergent properties for an empirical ecosystem model that has been validated by time series information. Using emergent properties from ecological network analysis as indices of ecosystem change would be useful for ecosystem management: if an index could signal a change in the system before the system changes it would be a useful tool. Unfortunately the network indices do not seem to lead the PDO, although large fluctuations from the average in these indices should be a cause for caution if enough is known about an ecosystem to get a long-term trend.

The Aleutian Islands and Southeast Alaska ecosystems have undergone many changes over the past 40 years. Specifically, in the Aleutians there was a shift after 1976 with a large decline in the main top predators (Steller sea lions, sharks and skates) and their prey (Atka mackerel and pollock), and concomitantly there was an increase in other predators such as halibut and arrowtooth flounder. In contrast, the Steller sea lion population in Southeast Alaska has been increasing although not at the same rate as the decline in the Aleutian Islands, and species such as herring, Pacific cod, halibut and arrowtooth flounder have also increased.

This difference in how the systems adapted to the environmental changes and human impacts is seen in the emergent properties of the systems. The large decline in most of the important species in the Aleutians (Steller sea lions, sharks and skates, Pacific Ocean perch, Atka mackerel, pollock and sablefish) after 1976 reduced the AMI and entropy, as the flows became more diverse. This is also seen by



**Figure 9.** Changes in the Finn Cycling Index (FCI). **A** FCI in Southeast Alaska (grey) and Aleutian Islands (black) and the 5 year running averages of those values in both systems (thicker lines). **B** The absolute percentage difference between the monthly FCI and running average FCI for the Aleutians (black) and Southeast Alaska (grey). Straight lines indicate the average percentage difference pre- and post-1976 and 1988.

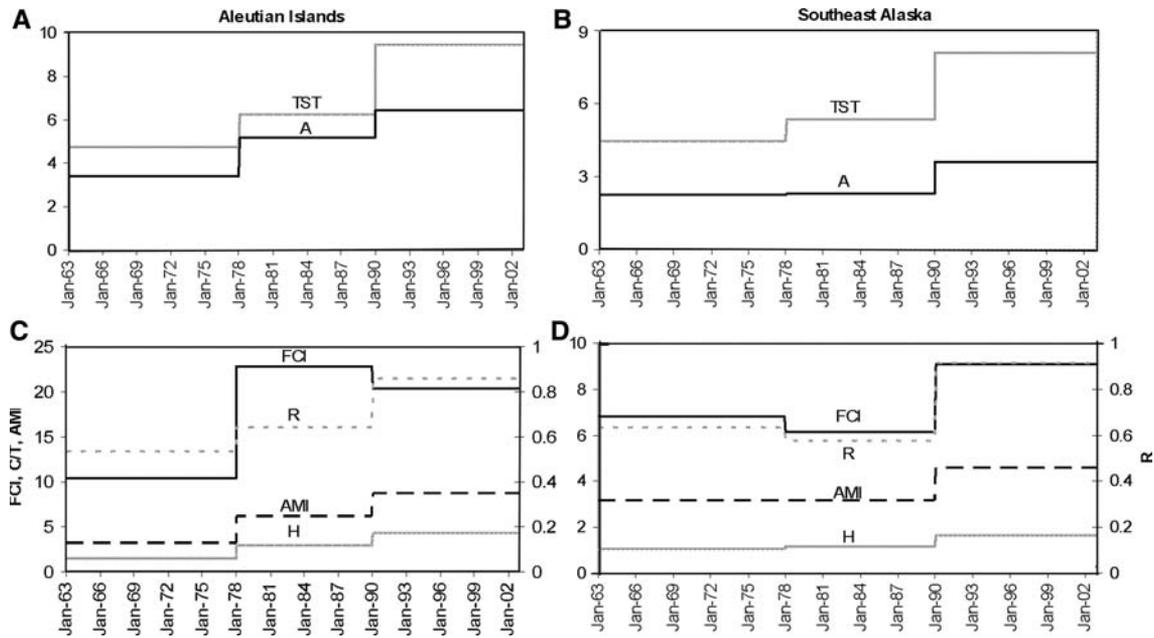
the increase in the redundancy at that time as the flow structure became more uncertain. In addition, the recycling (FCI) in the Aleutians declined after 1976, not only due to the reductions in the species mentioned above, but also due to the reduction in arrowtooth flounder. Arrowtooth flounder feed on discards and therefore would be important for recycling, indicating that the system had less capacity to hold nutrients at that time, and had therefore lost some maturity sensu Odum (1969). On the other hand, the increase in halibut and arrowtooth flounder after the mid-1980s increased recycling but reduced the redundancy in the system.

In Southeast Alaska, there was very little change in entropy, organization and recycling after 1976. This was probably due to an increase in some species that was cancelled by a decline in others, for example, there was an increase in Steller sea lions, herring, Pacific cod and halibut, while there were concomitant declines in salmon (in the model even if the data did now show it), Pacific Ocean perch

and sablefish. These changes caused the ecosystem to be more stable with regards to entropy, information (AMI) and recycling (FCI).

The emergent properties of Southeast Alaska showed very little change overall pre- and post-1976 (Figure 10 B, D), although its redundancy and recycling did show less instability after 1976 whereas that of the Aleutians was more unstable. Thus it seems that the 1976 event did not affect the Southeast Alaska system as much as it did the Aleutians, but the decline in redundancy (Figure 8A) probably caused the system to become more brittle and therefore the 1988 event had more of an effect.

By 1988 herring, Pacific cod, sablefish and halibut started stabilizing in Southeast Alaska and the model was unable to reproduce the increase in salmon and Steller sea lions after 1988. The increase in salmon seen in the data (Figure 3B) was probably due to changes that took place not only in Southeast Alaska, but elsewhere in their distribution, and that had an affect on the trend of Steller



**Figure 10.** Percentage change in Aleutian Islands and Southeast Alaska of various indices from their 5 year running average values averaged over the three time periods, 1963–1976, 1977–1988 and 1989–2002. **A** Total systems throughput (TST) and ascendency (A) in the Aleutians. **B** Total systems throughput (TST) and ascendency (A) in Southeast Alaska. **C** Finn cycling index (FCI), entropy (H), average mutual information (AMI) and redundancy (R) in the Aleutian Islands. **D.** Finn cycling index (FCI), entropy (H), average mutual information (AMI) and redundancy (R) in Southeast Alaska.

sea lions (Gu nette and others 2006). This change in the model is also seen in the entropy and redundancy of the model. The entropy and redundancy increased after 1988 as the flows started diversifying and the system became more resilient, while its ascendency declined. The 1988 shift also caused a change in the maturity of the Aleutian Islands, with its FCI increasing (due to the increase in discard feeding arrowtooth flounder and halibut) and the variations in that index declining after 1988. These changes in the emergent properties are mirrored by the flattening of the decline in Steller sea lions, and an increase in arrowtooth flounder and halibut (Figure 3A). Although the 1988 shift caused large fluctuations in the growth (TST) of the Aleutians, the effect it had on the system was not as severe as the 1976 shift.

In conclusion, studying the emergent properties of these two ecosystems over time has given us new insights into the effects that changes in single species abundances have on the emergent properties of the whole ecosystem. It explains why the decline in primary production induced by the changes in the PDO after 1976 had more effect on the important species such as Steller sea lions in the Aleutians than it had on the same species in Southeast Alaska after 1988, when there were

similar declines in primary production in that system. The different trajectories for important species such as Steller sea lions, halibut and arrowtooth flounder in the two ecosystems were noticeable and explained some of the emergent properties. The recycling, entropy and degrees of freedom in the Southeast Alaska system showed no large change prior to 1988, during the time that the Stellers, herring, Pacific cod and halibut increased, due to the concomitant decline in Pacific Ocean perch, sablefish and salmon. In contrast, there were large reductions in these indices during the decline in Stellers, sharks, Atka mackerel, pollock and arrowtooth flounder in the Aleutians because there was no simultaneous increase in other species at that time. The increase in halibut and arrowtooth flounder later in the time series was obviously not enough to negate the large decline in top predators and their prey. Thus, a decline in one of the important species of an ecosystem could have a detrimental effect on that ecosystem if there are no other species to replace it. This is important to know when managing systems that have reduced biodiversity and increased anthropogenic impacts. Finally, it seemed that the two shifts in environmental forces had very different effects on the two ecosystems, with the 1976 shift affecting the

Aleutian Islands system but not showing a large effect in Southeast Alaska. This could have been expected as the Aleutians had a much higher ascendancy prior to 1976 than Southeast Alaska did. In contrast, the 1988 shift was seen in the emergent properties of both systems, and the shift had a destabilizing effect on all the indices in both systems although in the Aleutians the 1988 shift was not as severe as that of 1976.

Future work on the network analysis indices of these and other ecosystems should include the effects of parameter uncertainty on the emergent properties. A possible way to include uncertainty in the estimates would be to run the models through a Monte Carlo simulation routine, based on the uncertainty of the input parameters, and to examine the effects on the emergent properties. It might be sufficient to only look at the indices that have shown the most difference in the two systems, for example, the entropy, FCI and redundancy. However, as explained in Guénette and others (2006) making changes in the input parameters of the model would cause the model to be less well fitted to the data as small changes in biomass, production or vulnerability parameters could have large effects on the biomass and catch trajectories estimated by the model. Thus, these changes would increase the SS goodness-of-fit measure and would not reproduce the trends seen in the data. Some other form of uncertainty measure might be needed to measure the significance of the differences seen here.

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