

*The following supplement accompanies the article*

## **The relative importance of fisheries, trophodynamic and environmental drivers in a series of marine ecosystems**

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### **Supplement. Summary of characteristics of the nine ecosystems**

In each section below, we briefly describe the 9 ecosystems we compared in terms of location, system type, key species and fisheries, important changes over time and key environmental influences. References for each summary are given at the end.

#### **Barents/Norwegian Seas**

The combined Barents and Norwegian seas ecosystem is located in the northeast Atlantic Ocean, west and north of Norway. The Norwegian Sea is a deep ocean while the Barents Sea is a shelf ocean. This upwelling system is dominated by purse seine and pelagic trawl fisheries for the pelagic species, with Atlantic herring *Clupea harengus* as the most important pelagic species. Atlantic cod *Gadus morhua* is the most important demersal species. The demersal/benthic species are targeted by trawl, longline, gill net and Danish seines. The herring stock collapsed in the late 1960s and did not recover fully until the 1990s. There have been 3 collapses of the capelin *Mallotus villosus* stock (1985, 1993, 2003), all followed by a rapid recovery of the stock. There was increased abundance of pelagic fish in the Norwegian Sea from 1995 to 2006 co-occurring with an increase in water temperature. The North

Atlantic Oscillation (NAO) determines the inflow strength of Atlantic water, which affects the water temperature and salinity. Further, this affects the amount of ice in the Barents Sea (Skjoldal et al. 2004, Sakshaug et al. 2009).

### **Eastern Scotian Shelf (Canada)**

The Eastern Scotian Shelf ecosystem is an area defined by the Maritimes Region Groundfish Survey of Northwest Atlantic Fisheries Organization (NAFO) Divisions 4VsW. It extends from the Laurentian Channel in the northeast to a line from Halifax, Nova Scotia, south to the shelf break in the southwest with an area of approximately 10000 km<sup>2</sup>. Traditionally, groundfish species such as Atlantic cod, haddock *Melanogrammus aeglefinus*, silver hake *Merluccius bilinearis*, pollock *Pollachius virens* and white hake *Urophycis tenuis* were fished in this temperate ecosystem, in addition to flatfish such as American plaice *Hippoglossoides platessoides*, yellowtail flounder *Limanda ferruginea*, witch flounder *Glyptocephalus cynoglossus*, winter flounder *Pseudopleuronectes americanus* and redfish *Sebastes fasciatus* and *S. mentella*. However, in the early 1990s many of the east coast cod fisheries, including that of the eastern Scotian Shelf, collapsed and were closed. For demersal fish species only the Atlantic halibut *Hippoglossus hippoglossus* longline fishery and some flatfish fisheries are currently operating on the eastern Scotian Shelf. The fishery has switched to lower trophic level invertebrates such as American lobster *Homarus americanus*, clams, sea scallop *Placopecten magellanicus*, snow crab *Chionoecetes opilio* and shrimp. These species have increased in abundance since the collapse of groundfish, probably owing to a combination of predator release and cooler water temperatures. The otter trawl was the primary trawl for groundfish and flatfishes. Other demersal trawls and a variety of gear (e.g. longline and gill nets) were also used. Shrimp trawls are used for shrimp, traps in the snow crab and lobster fisheries and dredges for clams and sea scallops.

Since the 1950s, exploitation of groundfish has been intense. In the early 1990s, the cod stock collapsed, other groundfish species experienced serious declines and the ecosystem switched from one dominated by demersal fishes to one dominated by forage species such as American sand lance *Ammodytes americanus* and *A. dubius*, herring and invertebrates such as shrimp, snow crab and clams. In addition, the grey seal *Halichoerus grypus* population increased exponentially since the early 1970s. There have been significant fishing impacts with decreases in fish size, trophic level and proportion of predatory fish. The hydrographic environment of the Scotian Shelf is governed largely by its location near the confluence of 3 major currents, a shelf current, which brings cool fresh water primarily from

the Gulf of St. Lawrence, the Labrador Current, which brings cold fresh water from the north along the edge of the shelf, and the Gulf Stream, which brings warm salty water from the south. The Gulf Stream does not contact the Scotian Shelf directly. However, Gulf Stream water mixes with Labrador Current water over the continental slope so that the water along the shelf edge (slope water) is cooler and fresher in the northeast and warmer and saltier in the southwest. Shelf-bottom is also an important factor affecting the hydrographic environment. It consists of a series of submarine banks and cross-shelf channels along the outer shelf and basins and troughs along the central shelf that limit and guide the near-bottom flow. The deep basins on the central shelf are directly influenced by the slope water, where the water properties are determined by interactions between the Labrador Slope Water Current (Breeze et al. 2002, Shackell & Frank 2003, 2007, Drinkwater & Gilbert 2004, Bundy 2005, Bundy & Fanning 2005, Choi et al. 2005, Frank et al. 2005, 2011, Zwanenburg et al. 2006, Head & Pepin 2010).

### **Western Scotian Shelf (Canada)**

The Western Scotian Shelf ecosystem is an area defined by the Maritimes Region Groundfish Survey of NAFO Divisions 4X. It extends from Halifax Line south to the shelf break in the southwest, then west into and including the Bay of Fundy. This is a temperate ecosystem and traditionally had the same fisheries as the eastern Scotian Shelf described above. This system has seen changes in species composition, with reductions in the biomass of groundfish and flatfish, increases in some invertebrates and expansion of grey seals from the eastern Scotian Shelf onto the western Scotian Shelf. These changes have been accompanied by reductions in mean weight and length at age for some key commercial fisheries stock. These changes are not as severe as those observed on the eastern Scotian Shelf. The western Scotian Shelf is subject to a similar hydrographic environment as the eastern Scotian Shelf. However, it is more influenced by the Gulf Stream, which brings warm salty water from the south. The Gulf Stream does not contact the Scotian Shelf directly. However, Gulf Stream water mixes with Labrador Current water over the continental slope so that the water along the shelf edge (Slope Water) is cooler and fresher in the northeast and warmer and saltier in the southwest. Furthermore the Bay of Fundy is subject to very large tides, ranging from a mean height of 6 m (maximum, 8 m) in the outer bay to a mean height of 11.9 m (maximum, 16 m) in the inner bay, the highest in the world. These high tides generate intense vertical mixing caused by bottom turbulence and generate high levels of marine productivity (Garrett et al. 1978, Breeze et al. 2002, Shackell & Frank

2003, 2007, Drinkwater & Gilbert 2004, Bundy 2005, Bundy & Fanning 2005, Choi et al. 2005, Frank et al. 2005, 2011, Zwanenburg et al. 2006, Head & Pepin 2010, Shackell et al. 2010).

### **Southern Gulf of St. Lawrence (Canada)**

The southern Gulf of St. Lawrence ecosystem studied here is actually the southern half of the full Gulf of St. Lawrence and is considered a temperate-boreal ecosystem. Its area is defined by the Gulf Region Groundfish Survey of NAFO Division 4T (southern edge of the Laurentian channel and adjoining shelf, excluding the St. Lawrence estuary). The ecosystem has an area of approximately 75000 km<sup>2</sup>. The fish community of the Gulf of St. Lawrence is composed of large populations of groundfish such as cod, plaice, white hake, and Greenland halibut *Reinhardtius hippoglossoides*, while spring-spawning and fall-spawning herring stocks, migratory mackerel *Scomber scombrus* and small diadromous fishes (rainbow smelt *Osmerus mordax* and gaspereau [alewife] *Alosa pseudoharengus*) dominate the pelagic system. Large invertebrates include snow crabs, lobsters, rock crabs *Cancer irroratus*, decapod shrimp and a variety of bivalves such as Stimpson surf clam *Mactromeris polynyma*, softshell clams.

Otter trawls and Danish and Scottish seines were the primary mobile gear for groundfish and flatfish fisheries beginning in the 1950s. There has also been a large fixed gear sector involving mainly longlines and gill nets, traps in the snow crab and lobster fisheries and dredges for clams and sea scallops. Since the 1950s, exploitation of groundfish has been intense. In the early 1990s, the cod stock collapsed, other groundfish species experienced serious declines and the ecosystem switched from one dominated by demersal fishes to one dominated by forage species such as sand lance, herring, and invertebrates such as shrimp, snow crab and clams. In addition, the grey seal population increased exponentially since the early 1970s. There have been significant fishing impacts with decreases in fish size, trophic level and proportion of predatory fish. The Gulf of St. Lawrence is considered an inland sea. With a drainage basin that includes the Great Lakes, the Gulf receives more than half of the freshwater inputs from the Atlantic Coast of North America. The southern portion of the Gulf includes waters of varied depths, from large expanses of shallows covered by cold water (<0 to 2°C) in the south to the more than 300 m deep Laurentian Channel, covered by warm (4°C) and salty bottom water. Bottom temperatures on the shallows are influenced by *in situ* cooling and the influx of Labrador shelf water. Changes in the extent and temperature of that cold water mass greatly influence the community composition of the system. The southern Gulf of St. Lawrence has the farthest regular annual extension

of sea ice in the north Atlantic during winter, yet largely has the warmest surface water temperatures in Atlantic Canada during the summer. The conditions in this unique setting are suitable for a highly diverse and productive biological community that is composed of a mixture of estuarine and marine, and subtropical to subarctic species (Dufour & Ouellet 2007, Benoit & Swain 2008, Swain & Chouinard 2008, Dufour et al. 2010, Ruppert et al. 2010; [www.glf.dfo-mpo.gc.ca/e0006090](http://www.glf.dfo-mpo.gc.ca/e0006090)).

## **Gulf of Maine**

The Gulf of Maine ecosystem is part of the Northeastern US Continental Shelf Large Marine Ecosystem. The Gulf of Maine is a large (~79000 km<sup>2</sup>) basin with an average depth of around 160 m. It contains 3 deeper basins and varied topography. It is bounded by Georges Bank to the south and southeast, and the Scotian Shelf to the east. Key species in this temperate ecosystem include groundfish such as Atlantic cod, haddock, redfishes, silver hake, red hake *Urophycis chuss*, pollock, goosefish *Lophius americanus* and white hake; flatfish such as yellowtail flounder, summer flounder *Paralichthys dentatus*, American plaice, witch flounder, winter flounder, windowpane flounder *Scophthalmus aquosus* and Atlantic halibut; elasmobranchs such as spiny dogfish *Squalus acanthias* and a number of skates; pelagics such as Atlantic herring, Atlantic mackerel, and butterfish *Peprilus triacanthus*; squids such as longfin squid *Doryteuthis pealeii* and short fin squid *Illex illecebrosus*; and scallops.

The otter trawl is the primary trawl for groundfish and flatfishes. Other demersal trawls and a variety of gear (e.g. longline and gill nets) are also used. Midwater trawls and purse seines are the primary fisheries methods used to fish pelagic species. Small-mesh otter trawls are used on squids, and scallop dredges are used on sea scallops. The system changed from one dominated by flatfish and gadids to one dominated by small pelagics and elasmobranchs. Also, the community shifted from a demersal one to a pelagic one. The major perturbations were: (1) the arrival and subsequent departure of the distant water (international) fleets, with an estimated 50% decline in fish biomass during this time period, and (2) the 200 mile (322 km) limit extended jurisdiction in 1977 combined with modernization and increased capacity of the domestic fleet, which reduced groundfish to historically low levels. Recently, there has also been a documented shift in some fish populations, probably due to a change in temperature. Zooplankton composition shifted between the 1980s and 1990s coinciding with a major change in surface layer salinity. Movement of deep slope water into the Gulf of Maine through the northeast channel carries a steady supply of nutrients, which is interrupted by summer stratification. Nutrient-poor Labrador Shelf water is occasionally transported from the north by intense

negative NAO, and intrusion of fresh water from ice melting in the Gulf of St. Lawrence and the Arctic has recently occurred (Schlitz & Cohen 1984, Uchupi & Austin 1987, Townsend et al. 2004, Nye et al. 2009, Lucey & Nye 2010).

### **Georges Bank**

Like the Gulf of Maine, Georges Bank is part of the Northeastern US Continental Shelf Large Marine Ecosystem. Georges Bank is a relatively large (44000 km<sup>2</sup>) submerged marine plateau. It is bounded by the Gulf of Maine and Scotian Shelf to the north, the Mid-Atlantic Bight to the southwest, and the continental shelf to the south and east. The key species and fisheries are the same as those listed above for the Gulf of Maine. Similarly, the important changes over time are the same in this ecosystem as in the Gulf of Maine; they were seen throughout the US Continental Shelf Large Marine Ecosystem. However, this area differs physically from the Gulf of Maine. Offshore upwelling along the shelf-slope break, vigorous tidal mixing and the generally clockwise pattern of its currents concentrates nutrients on Georges Bank making Georges Bank highly productive. Periods of stratification can occur seasonally and in localized areas, which can temporarily interrupt the nutrient cycle (Cohen et al. 1982, Schlitz & Cohen 1984, Backus 1987, Butman 1987, Uchupi & Austin 1987, Drinkwater & Mountain 1997, Fogarty & Murawski 1998, Garrison & Link 2000, Franks & Chen 2001, Townsend et al. 2004, Nye et al. 2009, Lucey & Nye 2010, Mountain & Kane 2010, Link et al. 2011).

### **Hecate Strait (Canada)**

The Hecate Strait ecosystem is defined by the Fisheries and Oceans Canada groundfish survey area between Haida Gwaii (formerly the Queen Charlotte Islands) and mainland British Columbia. The southerly limit is 52° 32' N; the northerly limit extends from Celestial Reef (approximately 54° 45' N, 131° 25' W) to Langara Island (approximately 54° 15' N, 133° 03' W; Olsen et al. 2009). This is predominantly a downwelling system; southerly winds dominate in winter and conversely, in summer, relaxation of downwelling winds produces a surface offshore flow and a deep onshore flow (Crawford et al. 1995, 2007). The Aleutian Low and the North Pacific High pressure systems are large-scale climate features that affect the Hecate Strait area (Crawford et al. 2007, Lucas et al. 2007). Physical forcing of primary production in this system includes enrichment by wind-driven upwelling (i.e.

weakened downwelling), estuarine flow of freshwater runoff and tidal and wind mixing (Lucas et al. 2007, Ware & McQueen. 2006a,b,c). Primary production is initiated in areas where shallow banks limit the depth of mixing (localized effect, Mackas et al. 2007). Primary producers are retained within Hecate Strait through recirculation by topography, relatively weak upwelling, the Haida G'waii (islands) barrier and mesoscale eddies (Lucas et al. 2007). Plankton (including euphausiids, which are important prey for marine fish, mammals and seabirds) are concentrated by bathymetric (bank edges) and hydrographic features and interactions with circulation (anticyclonic eddies, river plume fronts; Mackas et al. 2007). Fish species in Hecate Strait include forage species, such as Pacific herring *Clupea pallasii* and eulachon *Thaleichthys pacificus*; groundfish species, such as Pacific cod *Gadus macrocephalus*, sablefish *Anoplopoma fimbria*, lingcod *Ophiodon elongatus*, walleye pollock *Theragra chalcogramma* and Pacific hake *Merluccius productus*; flatfish species, such as arrowtooth flounder *Atheresthes stomias*, southern rock sole *Lepidopsetta bilineata*, Dover sole *Microstomus pacificus*, English sole *Parophrys vetulus*, rex sole *Glyptocephalus zachirus* and Pacific halibut *Hippoglossus stenolepis*; many rockfish species (e.g. yellowtail rockfish *Sebastes flavidus*, silvergray rockfish *S. brevispinus*, redbanded rockfish *S. babcocki*, canary rockfish *S. pinniger*, quillback rockfish *S. maliger*); and elasmobranch species, such as spiny dogfish, spotted ratfish *Hydrolagus colliei* and skate species (Lucas et al. 2007, Sinclair et al. 2007, Olsen et al. 2009).

Important commercial fisheries include fisheries for Pacific herring (northern Hecate Strait near Prince Rupert, British Columbia) and for pelagic and groundfish species. Pacific herring were overfished during the 1950s to early 1960s and recovered in the 1970s; current low biomass estimates of 2 of the 3 stocks are thought to be due to factors other than fishing (Schweigert et al. 2007). Most groundfish species of limited commercial value that are caught primarily as bycatch in groundfish fisheries showed an increasing trend over the entire time series with an approximate 4-fold increase in biomass. Two other groups (12 groundfish species) showed an initial period of increase, followed by a decline to the late 1990s, and an increase in the early 2000s. A final group that included Pacific cod and spiny dogfish showed a downward trend throughout the time series. Trends in biomass of commercially important groundfish species generally correspond to trends in fishing effort and a continuing increase in primary and secondary production. Abundance of some baleen whales (e.g. humpback whales *Megaptera novaeangliae*) and pinnipeds (e.g. Steller sea lions *Eumetopias jubatus*) has increased (Crawford et al. (1995), Gregr 2004, Heise et al. 2007). Important references for Hecate Strait include Ainsworth et al. (2002), Gregr (2004), Ware & McQueen (2006a,b,c), Lucas et al. (2007, and all associated appendices), Pearsall and Fargo (2007), Sinclair et al. (2007), Olsen et al. (2009).

## Gulf of Alaska

The Gulf of Alaska is a large (~300000 km<sup>2</sup>) relatively narrow continental shelf system with shallow banks incised by deep gullies. It is bordered to the west by the Aleutian Islands, to the north by Alaska and to the east by British Columbia, and extends into the deep basin to about 52° N latitude. The Gulf of Alaska continental shelf is an ice-free sub-Arctic system in which overall downwelling is driven by the strong Alaska Stream/subarctic gyre circulation, but seasonal and localized upwelling is driven by local winds and dynamic current/bathymetry interactions. Steller sea lions are the primary pinnipeds. Dominant groundfish include arrowtooth flounder, walleye pollock, Pacific cod, Pacific halibut, Pacific ocean perch *Sebastes alutus* and other rockfish, with sablefish and grenadiers in the slope regions. Skates, dogfish, sculpins, and a variety of small flatfish are also present. Dominant pelagics include capelin, eulachon, Pacific herring and Pacific salmon species with other small pelagics important seasonally and locally. Scallops and shrimp are locally abundant; crab populations are depressed.

Pelagic trawl fisheries for pollock, bottom trawl fisheries for cod and flatfish, longline fisheries for cod, sablefish, and halibut, and pot fisheries for cod comprise the groundfish fleet. Many local salmon fisheries are prosecuted with gill nets, and herring fisheries with purse seines and other methods. Human exploitation in this ecosystem was subsistence only before the mid-1700s. Sea otters *Enhydra lutris* were hunted from 1742 to 1910, fur seals were hunted at sea from 1860 to 1910 and extensive whaling took place from 1835 to 1848 (right whales *Eubalaena japonica*), 1907 to 1939 (shore whaling) and 1946 to 1979 (at-sea whaling). Large scale commercial salmon and herring fishing began in the late 1800s and early 1900s. Pacific halibut fishing began in 1915. Large-scale groundfish and crab fishing began in 1960; groundfish fishing continues to the present, while crab and shrimp fisheries declined around 1980 and never recovered. A major change in community composition at multiple trophic levels was observed around 1977 and has been attributed to a climate regime shift. However, physical mechanisms driving dynamics have proven elusive in the Gulf of Alaska. Arrowtooth flounder populations have increased since the 1960s, while walleye pollock peaked and declined in that time. Steller sea lions declined from the 1970s through the early 2000s, but populations appear to have stabilized in the Gulf.

The Pacific Decadal Oscillation is an atmosphere–ocean pattern observed across the North Pacific and linked to zooplankton and salmon productivity in the oceanic Gulf of Alaska. Local weather patterns are also influenced by El Niño Southern Oscillation (ENSO). Locally varying conditions lead



to complex and dynamic influences in various regions of the continental shelf. The position and strength of the Alaska Stream and its interaction with bottom topography is thought to alter the nutrient supply to phytoplankton on the shelf, along with seasonal, wind-driven, cross-shelf (Ekman) transport and entrainment due to freshwater runoff. Both seasonal downwelling and upwelling occur locally on the continental shelf as a result of the interactions of currents, runoff and seasonally as well as locally varying winds (Hood & Zimmerman 1986, Stabeno et al. 2004, Gaichas 2006, Gaichas et al. 2011).

### **Eastern Bering Sea**

The Eastern Bering Sea is a broad (>500 km), shallow (<200m), large (~500000 km<sup>2</sup>) area of continental shelf bounded by a deep basin and the Aleutian Islands to the southwest, the Alaska Peninsula to the southeast, Russian waters to the northwest and St. Matthew Island and mainland Alaska to the north and northeast. This ecosystem is transitional between Arctic and subArctic; it has weak tide and wind-driven circulation with substantial seasonal ice influence. Northern fur seals and Steller sea lions are the primary pinnipeds. Dominant groundfish include walleye pollock, Pacific cod, yellowfin sole *Limanda aspera*, Northern rock sole *Lepidopsetta polyxystra*, flathead sole *Hippoglossoides elassodon*, arrowtooth flounder, Alaska plaice *Pleuronectes quadrituberculatus* and skates. Rockfish, sablefish and Pacific halibut are also present. Dominant pelagics include Pacific herring and Pacific salmon with capelin and other small pelagics important seasonally and locally; major invertebrates include king crabs *Paralithodes camtschaticus* and snow crabs.

Pelagic trawl fisheries for pollock, bottom trawl fisheries for cod and flatfish, and longline and pot fisheries for cod comprise the groundfish fleet. Crabs are fished with pots. Bristol Bay salmon fisheries are prosecuted with gill nets, and Togiak herring fisheries with purse seines and other methods. Human exploitation was subsistence only before the late 1700s. Fur seal hunting spanned from 1786 to 1984, with extensive whaling and walrus *Odobenus rosmarus* hunting occurring from 1845 to 1915. Large-scale commercial fishing commenced around 1950 and continues to the present, with a 2 million t harvest cap on groundfish achieved annually in recent years. A majority of commercial fishery tonnage depends on walleye pollock production, which in turn is hypothesized to be closely tied to climate and sea ice dynamics. A recent stretch of anomalously warm years with early ice retreat resulted in low zooplankton biomass and poor pollock production from 2001 to 2005, while cooler years with late ice retreat from 2007 to 2010 resulted in higher zooplankton biomass, improved pollock production and improved reproductive success for seabirds. However, northern fur seal pup production has declined

steadily since the 1960s. The North Pacific Index (NPI) measures the strength of the Aleutian Low, which relates to wintertime temperatures over the Bering Sea. This region is also influenced by the ENSO and the Arctic Oscillation (AO). These climate drivers combined with local conditions influence the timing of ice formation and retreat on the Bering Sea shelf, which is critical to setting up conditions for biological productivity across most trophic levels. Warm conditions associated with early ice retreat and late water column stratification favor later zooplankton blooms and more pelagic production, while in cold years with late ice retreat, stratification happens immediately, promoting blooms that sink to the benthic energy food web. Implications for individual species depend on overwinter survival and predation impacts (Loughlin & Ohtani 1999, Aydin & Mueter 2007, Zador & Gaichas 2010, Hunt et al. 2011).

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