

Contrasting ecological impacts of native and non-native marine crabs: a global meta-analysis

Brett R. Howard*, Thomas W. Therriault, Isabelle M. Côté

*Corresponding author: brett.howard@sfu.ca

Marine Ecology Progress 577: 93–103 (2017)

- Figure S1. Literature selection results
- Figure S2. Funnel plots for publication bias testing
- Figure S3. Cumulative forest plots for publication bias testing

- Table S1. Survey of invasive marine and euryhaline crab introductions, www.int-res.com/articles/suppl/m577p093_supp.xls
- Table S2. Table of individual experiments used for meta-analysis, www.int-res.com/articles/suppl/m577p093_supp.xls
- Table S3. Descriptive table for moderator levels
- Table S4. Average carapace widths (mm) of crab species included in meta-analysis
- Table S5. Summary comparison of results from full and large-studies-only analyses
- Table S6. Summary comparison of results from analyses with and without studies of European green crab (*Carcinus maenas*)

- Literature used in meta-analysis

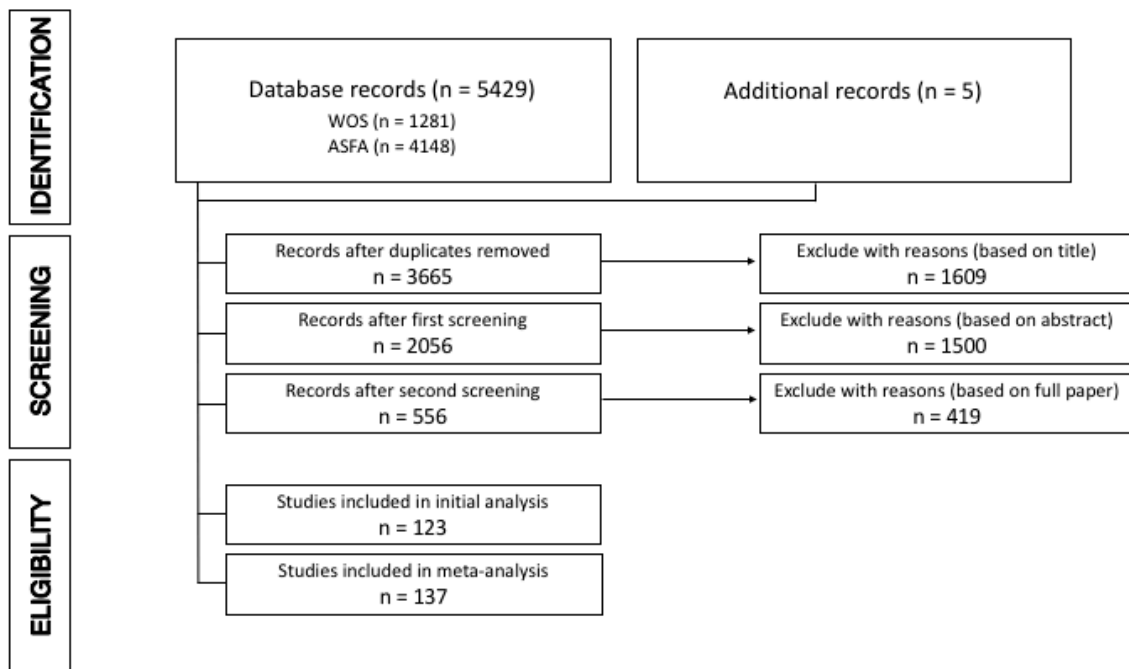


Figure S1. Summary of literature selection results. Sample sizes (n) are shown for each step of the systematic search. WOS: Web of Science; ASFA: Aquatic Science and Fisheries Abstracts.

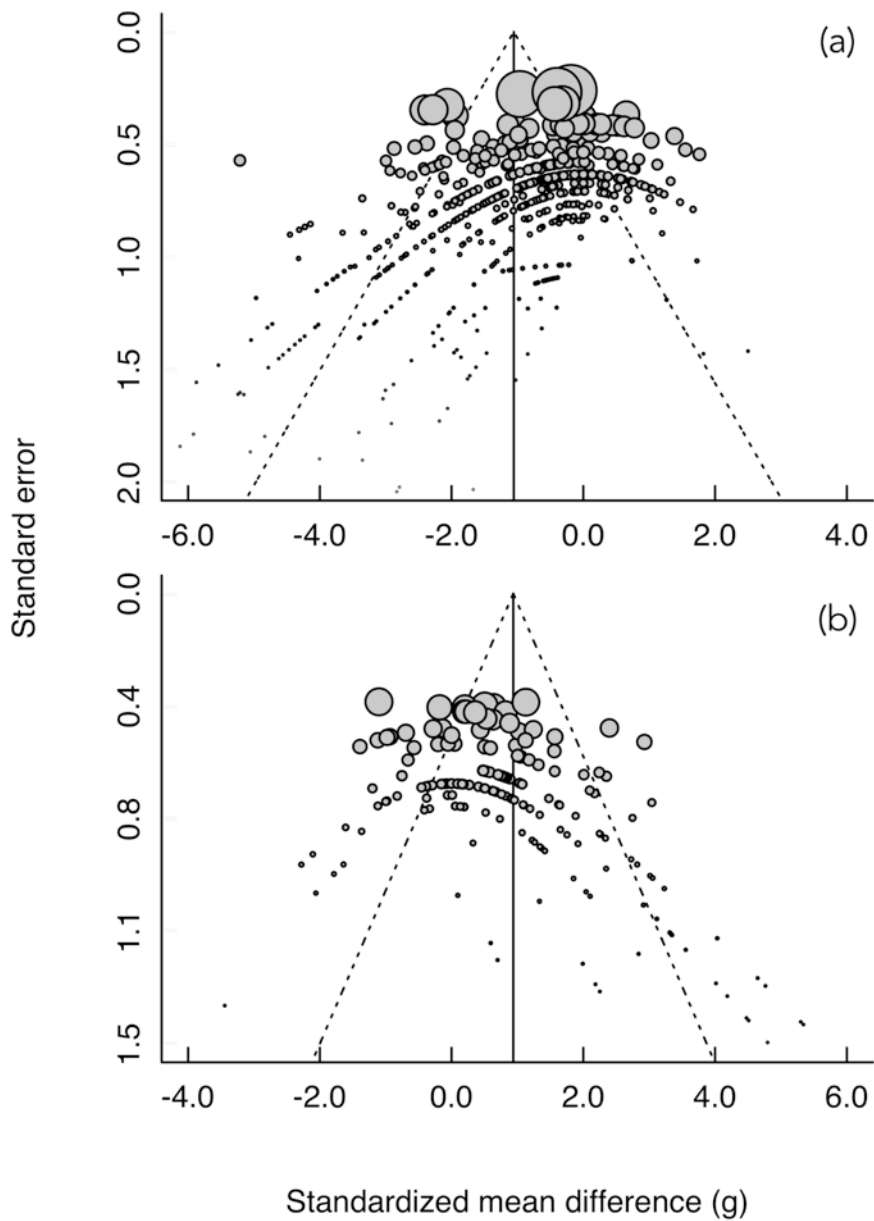


Figure S2. Funnel plots relating standard error to effect size for experiments of (a) direct effects and (b) indirect effects of crabs on responding species. Point size represents the weight of the experiment, calculated as the inverse of the sample variance (Viechtbauer 2010). Dashed lines represent the 95% CI. The asymmetric shape of the funnels suggests publication bias against small, non-significant experiments.

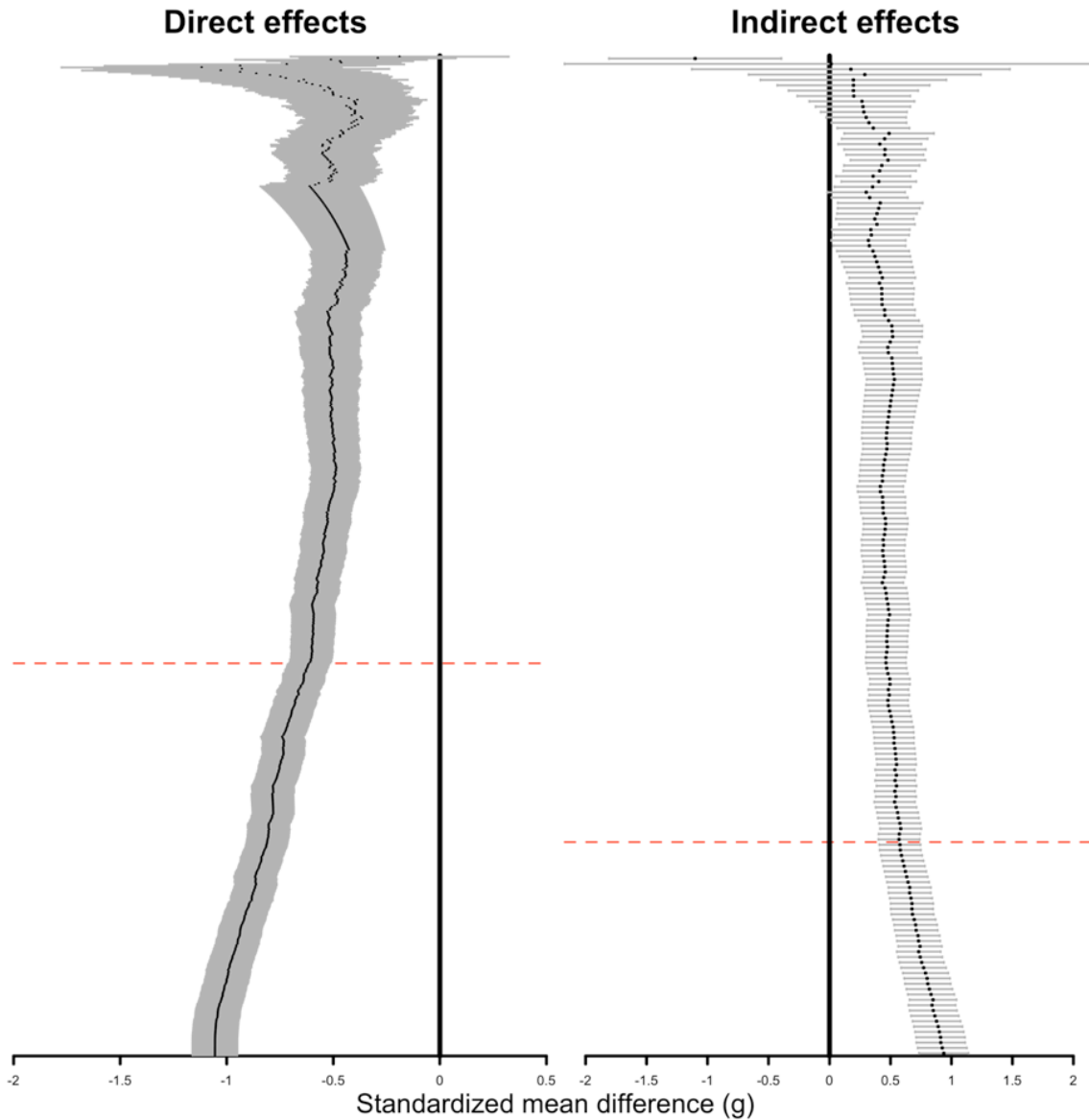


Figure S3. Cumulative forest plots for experiments reporting direct and indirect interactions between crabs and prey, added in order of smallest (top) to largest (bottom) variance. Horizontal red lines indicate approximate variance values at which small studies start to shift the effect size. These thresholds were estimated visually at values of 0.73 for studies of direct effects of crabs and 1.02 for studies of indirect effects. Studies with variances smaller than these thresholds were included in “large-studies-only” datasets.

Table S3. Description of moderator levels

Moderator	Level	Description	n (overall dataset)
Interaction type	Direct	Experiment tests a direct, consumptive interaction between a crab and responding species. Interaction either known or strongly expected to be direct by the original authors.	647
	Indirect	Experiment tests an indirect interaction between a crab and responding species. Interaction either known or strongly expected to be indirect by the original authors. Mechanism of interaction typically assumed to be a trophic cascade, however we did not require this to be demonstrated.	187
Crab origin	Native	Crab species is confirmed to be native to the region.	292
	Non-native	Crab species is introduced, invasive, or otherwise being tested against responding species that is does not co-occur with naturally.	542
Prey functional group	Mobile infauna	Clams, marine worms, and infaunal crustaceans (amphipods and isopods).	246
	Mobile epifauna	Surface-dwelling decapods (including hermit crabs, shrimps, etc.), gastropods, scallops, and mobile echinoderms.	189
	Primary producers	Seaweeds, seagrasses, and phytoplankton.	123
	Sessile invertebrates	Mussels, oysters, barnacles, and other encrusting epifauna.	263
	Vertebrates	Limited to birds and fish.	13
Experimental design	Natural field experiments	No species controlled experimentally (including crab). Without- and with-crab “treatments” are a result of spatial or temporal changes in crab presence (e.g. before/after an introduction or spatially different abundances of crab).	22
	Unstocked enclosures	Field enclosures or exclosures where only the crab species was manipulated experimentally while the remainder of the community was left undisturbed.	256
	Stocked enclosures	Field enclosures or exclosures where densities of one or multiple responding species were manipulated along with crab presence, while remainder of the community was left undisturbed.	152
	Laboratory mesocosm	A closed or mostly closed laboratory-based mesocosm requiring a minimum of two trophic levels and three species. Densities of all species, including crab, were controlled by the original authors.	193
	Predation experiment	Only one crab predator and one prey species or type (e.g. two species of mussel) in a closed laboratory system. This setup excluded indirect interactions as they tested direct predation only.	211

Table S4. Reported average carapace widths (mm) of all crab species included in the meta-analysis. See Table S2 for the native/non-native status of crab species.

Crab species	Carapace width (mm)	Source
<i>Acanthocyclus gayi</i>	24.0	Garth (1957)
<i>Acanthocyclus hassleri</i>	25.0	Rathbun (1930)
<i>Achelous spinimanus</i>	110.0	Williams (1984)
<i>Callinectes sapidus</i>	168.0	Williams (1984)
<i>Cancer antennarius</i>	118.0	Rathbun (1930)
<i>Cancer borealis</i>	143.0	Williams (1984)
<i>Cancer irroratus</i>	119.0	Williams (1984)
<i>Cancer pagurus</i>	130.0	Ingle (1997)
<i>Cancer productus</i>	157.5	Rathbun (1930)
<i>Caphyra rotundifrons</i>	13.0	Jenkins (2012)
<i>Carcinus aestuarii</i>	65.0	sealifebase.org
<i>Carcinus maenas</i>	79.4	Rathbun (1930)
<i>Cyclograpsus lavauxi</i>	28.0	McLay (1988)
<i>Dotilla fenestrata</i>	12.0	Hartnoll (1973)
<i>Dyspanopeus sayi</i>	29.7	Williams (1984)
<i>Dyspanopeus texanus</i>	27.0	Rathbun (1930)
<i>Eurypanopeus depressus</i>	25.0	Williams (1984)
<i>Eurytium limosum</i>	43.0	Williams (1984)
<i>Grapsus grapsus</i>	80.0	eol.org
<i>Hemigrapsus sanguineus</i>	42.0	Richerson (2017)
<i>Heterozius rotundifrons</i>	23.0	McLay (1988)
<i>Hyas araneus</i>	76.5	Miller & O'Keefe (1981)
<i>Liocarcinus depurator</i>	51.0	Hayward & Ryland (1995)
<i>Macrocoeloma diplacanthum</i>	12.8	Rathbun (1925)
<i>Menippe adina</i>	10.0	tpwd.texas.gov
<i>Menippe mercenaria</i>	129.0	Williams (1984)
<i>Mennipe nodifrons</i>	72.0	Rathbun (1930)
<i>Metacarcinus gracilis</i>	91.0	Rathbun (1930)
<i>Metacarcinus magister</i>	198.0	Rathbun (1930)
<i>Micropanope sp.</i>	6.5	Williams (1984)
<i>Mictyris longicarpus</i>	25.0	ala.org.au
<i>Mithraculus forceps</i>	38.0	Williams (1984)
<i>Mithraculus sculptus</i>	26.4	Rathbun (1925)
<i>Necora puber</i>	109.0	Hearn (2002)
<i>Neohelice granulata</i>	32.0	Angeletti & Cervellini (2015)
<i>Ovalipes catharus</i>	150.0	McLay (1988)
<i>Ovalipes ocellatus</i>	87.0	Williams (1984)
<i>Pachygrapsus crassipes</i>	48.0	eol.org.au
<i>Pachygrapsus transversus</i>	26.4	Williams (1984)
<i>Panopeus herbstii</i>	62.0	Williams (1984)
<i>Paragrapsus gaimardii</i>	48.0	Campbell & Griffin (1966)
<i>Percnon gibbesi</i>	28.0	Williams (1984)
<i>Petrolisthes armatus</i>	14.0	Masterson (2007)
<i>Pilumnus caribaeus</i>	21.6	Rathbun (1930)
<i>Rhithropanopeus harrisi</i>	21.3	Williams (1984)

<i>Sesarma reticulatum</i>	28.0	Williams (1984)
<i>Trapezia rufopunctata</i>	28.0	Poupin & Juncker (2010)
<i>Uca annulipes</i>	18.5	Crane (1975)
<i>Uca polita</i>	25.0	Crane (1975)
<i>Uca pugilator</i>	26.0	Williams (1984)
<i>Uca pugnax</i>	23.0	Williams (1984)
<i>Uca vocans</i>	22.5	Crane (1975)
<i>Uca vomeris</i>	27.0	Crane (1975)

REFERENCES

- ala.org.au (2017) *Mictyris longicarpus* Latreille, 1806 (n.d.) Retrieved from <https://www.ala.org.au/>
- Angeletti S, Cervellini P (2015) Population structure of the burrowing crab *Neohelice granulata* (Brachyura, Varunidae) in a southwestern Atlantic salt marsh. *Lat Am J Aquat Res* 43:539–547
- Campbell BM, Griffin DJG (1966) The Australian Sesarminae (Crustacea : Brachyura): Genera *Helice*, *Helograpsus* nov., *Cyclograpus*, and *Paragrapsus*. *Memoirs of the Queensland Museum* 14:127–174
- Crane J (1975) Fiddler crabs of the world (Ocypodidae: genus *Uca*). Princeton University Press., Princeton, N.J.
- eol.org (2017) Sally Lightfoot Crab (n.d.) Retrieved from <http://eol.org/pages/1021865/details>
- eol.org (2017) Lined Shore Crab (n.d.) Retrieved from <http://eol.org/pages/317367/details>
- Garth JS (1957) The Crustacea Decapoda Brachyura of Chile. Reports of the Lund University Chile expedition 1948-1949. *Lunds Universitets Arsskrift.*, Lund, 134 pp.
- Hartnoll RG (1973) Factors affecting the distribution and behaviour of the crab *Dotilla fenestrata* on East African shores. *Estuar Coast Mar Sci* 1:137–152
- Hayward PJ, Ryland JS (1995) Handbook of the marine fauna of north-west Europe. Oxford University Press., Oxford, 880 pp.
- Hearn AR (2002) The transport chain of velvet crabs from Orkney, the Western Isles and Northumberland to Spain. Sea Fish Industry Authority., Edinburgh, 50 pp.
- Ingle RW (1997) Crayfishes, lobsters, and crabs of Europe: An illustrated guide to common and traded species. Chapman & Hall., London, 289 pp.
- Jenkins P (2012) *Caphyra rotundifrons*: Turtle-weed crab. Retrieved from <http://www.gbri.org.au/Classes/2012/Caphyrotundifrons|PhilippaJenkins.aspx>
- McLay CL (1988) Brachyura and crab-like anomura of New Zealand. University of Auckland., Auckland, 419 pp.
- Miller RJ, O'Keefe P (1981) Seasonal and depth distribution, dize, and molt cycle of the Spider Crabs, *Chionoecetes opilio*, *Hyas araneus*, and *Hyas coarctatus* in a Newfoundland Bay. *Can. Fish. Aquat. Sci. Tech. Rep.* 1003.
- Rathbun MJ (1925) The spider crabs of America. *Bulletin of the United States National Museum* 129., Washington DC, 200 pp.
- Rathbun MJ (1930) The Cancroid crabs of America of the families Euryalidae, Portunidae, Atecyclidae, Cancridae and Xanthidae. *Bulletin of the United States National Museum* 152., Washington DC, 609 pp.
- Richerson MM (2017) *Hemigrapsus sanguineus*. USGS Nonindigenous Aquatic Species Database, Gainesville, FL. Retrieved from <https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=183>
- Sealifebase.org (2017) *Carcinus aestuarii* Nardo, 1847 Mediterranean shore crab (n.d.). Retrieved from <http://www.sealifebase.org/summary/Carcinus-aestuarii.html>
- Masterson J (2007) Green Porcelain Crab. Retrieved from http://www.sms.si.edu/irlspec/Petrolisthes_armatus.htm

Poupin J, Juncker M (2010) A guide to the decapod crustaceans of the South Pacific. CRISP and SPC., Noumea, New Caledonia, 320 pp.

tpwd.texas.gov (2017) Gulf Stone Crab (*Menippe adina*) (n.d.) Retrieved from <http://tpwd.texas.gov/huntwild/wild/species/stonecrab/>

Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press., Washington DC, 566 pp.

Table S5. Summary comparison of results from analyses of the full and large-studies-only datasets. Differences are highlighted in bold. NS indicates a statistically non-significant result.

Results of the full dataset	Remains true with large-studies-only data?
Direct and indirect effects were significant in opposing directions	Yes
Direct effects dataset	
No significant difference between the direct effects of non-native and native crabs	Yes
Significant differences in effect size among different experimental designs	Yes
All experimental designs have a significantly negative effect on prey abundance	Yes
Experimental designs with the strongest effects are laboratory mesocosms and single-species predation experiments	Natural experiments now have the strongest effect
Non-native crabs reduced prey abundance significantly more than native crabs in laboratory mesocosms	Yes
Significant differences in effect size among prey functional groups	Yes
All prey functional groups were significantly negatively affected by crab predation	Yes, except for vertebrates (now NS because of small sample size)
Non-native crabs reduced abundance of primary producers significantly more than predation by native crabs	Trend same but NS
Native crabs reduced abundance of mobile epifauna significantly more than predation by non-native crabs	Yes
Indirect effects dataset	
No significant difference between the indirect effects of non-native and native crabs	Yes
No significant difference in effect size among different experimental designs	Yes
Mesocosm experiments had the only significant effect on responding species abundance	Stocked enclosures and mesocosms now both significant
Non-native crabs increased basal prey abundance significantly more in unstocked field enclosures than did native crabs	Yes
Significant differences in effect size among prey functional groups	Yes
Effect sizes for sessile invertebrates and primary producers were both significantly positive	Yes
Non-native crabs increased abundance of primary producers significantly more than native crabs	Yes

Table S6. Summary comparison of results from analyses with and without studies of European green crab (*Carcinus maenas*). Differences are highlighted in bold. NS indicates a statistically non-significant result.

Results of the full dataset	Remains true when green crab studies removed?
Direct and indirect effects were significant in opposing directions	Yes
Direct effects dataset	
No significant difference between the direct effects of non-native and native crabs	Yes
Significant differences in effect size among different experimental designs	Yes
All experimental designs have a significantly negative effect on prey abundance	Yes
Experimental designs with the strongest effects are laboratory mesocosms and single-species predation experiments	Yes
Non-native crabs reduced prey abundance significantly more than native crabs in laboratory mesocosms	Yes
Significant differences in effect size among prey functional groups	Yes
All prey functional groups were significantly negatively affected by crab predation	Yes
Non-native crabs reduced abundance of primary producers significantly more than predation by native crabs	Trend same but NS
Native crabs reduced abundance of mobile epifauna significantly more than predation by non-native crabs	Yes
Indirect effects dataset	
No significant difference between the indirect effects of non-native and native crabs	No
No significant differences in effect size among different experimental designs	No
Mesocosm experiments had the only significant effect on responding species abundance	Yes
Non-native crabs increased basal prey abundance significantly more in unstocked field enclosures than did native crabs	Insufficient sample size to test for this difference
Significant differences in effect size among prey functional groups	Yes
Effect sizes for sessile invertebrates and primary producers were both significantly positive	Yes
Non-native crabs increased abundance of primary producers significantly more than native crabs	Trend same but NS

Literature used in meta-analysis

- Abdullah MM, Lee SY (2016) Meiofauna and crabs in mangroves and adjoining sandflats: Is the interaction physical or trophic? *J Exp Mar Bio Ecol* 479:69–75
- Addison B (2009) Shell traits of a marine mussel mediate predation selectivity by crabs and sea stars. *J Shellfish Res* 28:299–303
- Alberti J, Escapa M, Iribarne O, Silliman B, Bertness M (2008) Crab herbivory regulates plant facilitative and competitive processes in Argentinean marshes. *Ecology* 89:155–64
- Ambrose Jr. WG (1984) Increased emigration of the amphipod *Rhepoxynius abronius* (Barnard) and the polychaete *Nephtys caeca* (Fabricius) in the presence of invertebrate predators. *J Exp Mar Bio Ecol* 80:67–75
- Armitage AR, Fong P (2006) Predation and physical disturbance by crabs reduce the relative impacts of nutrients in a tidal mudflat. *Mar Ecol Prog Ser* 313:205–213
- Aschaffenburg MD (2008) Different crab species influence feeding of the snail *Nucella lapillus* through trait-mediated indirect interactions. *Mar Ecol* 29:348–353
- Barbeau MA, Scheibling RE (1994a) Procedural effects of prey tethering experiments: Predation of juvenile scallops by crabs and sea stars. *Mar Ecol Prog Ser* 111:305–310
- Barbeau MA, Scheibling RE (1994b) Temperature effects on predation of juvenile sea scallops [*Placopecten magellanicus* (Gmelin)] by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say). *J Exp Mar Bio Ecol* 182:27–47
- Bertness MD, Holdredge C, Altieri AH (2009) Substrate mediates consumer control of salt marsh cordgrass on Cape Cod, New England. *Ecology* 90:2108–17
- Bertness MD, Coverdale TC (2013) An invasive species facilitates the recovery of salt marsh ecosystems on Cape Cod. *Ecology* 94:1937–1943
- Bishop MJ, Wear SL (2005) Ecological consequences of ontogenetic shifts in predator diet: Seasonal constraint of a behaviorally mediated indirect interaction. *J Exp Mar Bio Ecol* 326:199–206
- Blasi JC, O'Connor NJ (2016) Amphipods as potential prey of the Asian shore crab *Hemigrapsus sanguineus*: Laboratory and field experiments. *J Exp Mar Bio Ecol* 474:18–22
- Bourdeau PE (2012) Morphological defense influences absolute, not relative, nonconsumptive effects in marine snails. *Behav Ecol* 24:505–510
- Brousseau D, Goldberg R (2007) Effect of predation by the invasive crab *Hemigrapsus sanguineus* on recruiting barnacles *Semibalanus balanoides* in western Long Island Sound, USA. *Mar Ecol Prog Ser* 339:221–228
- Brousseau D, Goldberg R, Garza C (2014) Impact of predation by the invasive crab *Hemigrapsus sanguineus* on survival of juvenile blue mussels in western Long Island Sound. *Northeast Nat* 21:119–133
- Bruno JF, O'Connor MI (2005) Cascading effects of predator diversity and omnivory in a marine food web. *Ecol Lett* 8:1048–1056
- Byers JE, Smith RS, Weiskel HW, Robertson CY (2014) A non-native prey mediates the effects of a shared predator on an ecosystem service. *PLoS One* 9:e93969
- Canuel EA, Spivak AC, Waterson EJ, Duffy JE (2007) Biodiversity and food web structure influence short-term accumulation of sediment organic matter in an experimental seagrass system. *Limnol Oceanogr* 52:590–602
- Carrasco SA, Phillips NE (2012) Differential vulnerability to predation in two sympatric whelks is mediated by juvenile traits. *Invertebr Biol* 131:187–196
- Casariago, Agustina M, Alberti J, Luppi T, Iribarne O (2008) Stage-dependent interactions between intertidal crabs: from facilitation to predation. *J Mar Biol Assoc United Kingdom* 89:781–788
- Christensen HT, Dolmer P, Petersen JK, Tørring D (2012) Comparative study of predatory responses in blue mussels (*Mytilus edulis* L.) produced in suspended long line cultures or collected from natural bottom mussel beds. *Helgol Mar Res* 66:1–9
- Christofolletti RA, Murakami VA, Oliveira DN, Barreto RE, Flores AA V (2010) Foraging by the omnivorous crab *Pachygrapsus transversus* affects the structure of assemblages on sub-tropical rocky shores. *Mar Ecol Prog Ser* 420:125–134

- Clemente S, Hernández JC, Montaña-Moctezuma G, Russell MP, Ebert TA (2013) Predators of juvenile sea urchins and the effect of habitat refuges. *Mar Biol* 160:579–590
- David Smith L, Hines AH (1991) The effect of cheliped loss on blue crab *Callinectes sapidus* Rathbun foraging rate on soft-shell clams *Mya arenaria* L. *J Exp Mar Bio Ecol* 151:245–256
- Davidson A, Griffin JN, Angelini C, Coleman F, Atkins RL, Silliman BR (2015) Non-consumptive predator effects intensify grazer-plant interactions by driving vertical habitat shifts. *Mar Ecol Prog Ser* 537:49–58
- deRivera CE, Ruiz GM, Hines AH, Jivoff P (2005) Biotic resistance to invasion: Native predator limits abundance and distribution of an introduced crab. *Ecology* 86:3364–3376
- Dernbach EM, Freeman AS (2015) Foraging preference of whelks *Nucella lapillus* is robust to influences of wave exposure and predator cues. *Mar Ecol Prog Ser* 540:135–144
- Donovan DA, Danko JP, Carefoot TH (1999) Functional significance of shell sculpture in gastropod molluscs: Test of a predator-deterrent hypothesis in *Ceratostoma foliatum* (Gmelin). *J Exp Mar Bio Ecol* 236:235–251
- Douglass JG, Duffy JE, Bruno JF (2008) Herbivore and predator diversity interactively affect ecosystem properties in an experimental marine community. *Ecol Lett* 11:598–608
- Douglass JG, Duffy JE, Spivak AC, Richardson JP (2007) Nutrient versus consumer control of community structure in a Chesapeake Bay eelgrass habitat. *Mar Ecol Prog Ser* 348:71–83
- Dye AH, Lasiak TA (1986) Microbenthos, meiobenthos and fiddler crabs: Trophic interactions in a tropical mangrove sediment. *Mar Ecol Ser* 32:259–264
- Ellis JC, Shulman MJ, Wood M, Witman JD, Lozynyak S (2007) Regulation of intertidal food webs by avian predators on New England rocky shores. *Ecology* 88:853–63
- Epelbaum A, Pearce CM, Barker DJ, Paulson A, Therriault TW (2009) Susceptibility of non-indigenous ascidian species in British Columbia (Canada) to invertebrate predation. *Mar Biol* 156:1311–1320
- Ericson J, Ljunghager F, Gamfeldt L (2009) Are there direct and cascading effects of changes in grazer and predator species richness in a model system with heterogeneously distributed resources? *Mar Biodivers* 39:71–81
- Estelle V, Grosholz ED (2012) Experimental test of the effects of a non-native invasive species on a wintering shorebird. *Conserv Biol* 26:472–81
- Fagerli CW, Norderhaug KM, Christie H, Pedersen MF, Fredriksen S (2014) Predators of the destructive sea urchin *Strongylocentrotus droebachiensis* on the Norwegian coast. *Mar Ecol Prog Ser* 502:207–218
- Feehan CJ, Francis FTY, Scheibling RE (2014) Harboring the enemy: Kelp holdfasts protect juvenile sea urchins from predatory crabs. *Mar Ecol Prog Ser* 514:149–161
- Feldman KL, Armstrong DA, Eggleston DB, Dumbauld BR (1997) Effects of substrate selection and post-settlement survival on recruitment success of the thalassinidean shrimp *Neotrypaea californiensis* to intertidal shell and mud habitats. *Mar Ecol Prog Ser* 150:121–136
- Fernandes T., Huxham M, Piper S. (1999) Predator caging experiments: A test of the importance of scale. *J Exp Mar Bio Ecol* 241:137–154
- Fodrie FJ, Kenworthy MD, Powers SP (2008) Unintended facilitation between marine consumers generates mortality for their shared prey. *Ecology* 89:3268–3274
- Forsström T, Fowler AE, Manninen I, Vesakoski O (2015) An introduced species meets the local fauna: predatory behavior of the crab *Rhithropanopeus harrisi* in the Northern Baltic Sea. *Biol Invasions* 17:2729–2741
- Freeman AS, Hamer CE (2009) The persistent effect of wave exposure on TMIs and crab predation in *Nucella lapillus*. *J Exp Mar Bio Ecol* 372:58–63
- Freeman AS, Wright JT, Hewitt CL, Campbell ML, Szeto K (2013) A gastropod's induced behavioral and morphological responses to invasive *Carcinus maenas* in Australia indicate a lack of novelty advantage. *Biol Invasions* 15:1795–1805
- Freeman AS, Dernbach E, Marcos C, Koob E (2014) Biogeographic contrast of *Nucella lapillus* responses to *Carcinus maenas*. *J Exp Mar Bio Ecol* 452:1–8
- Freeman AS, Frischeisen A, Blakeslee AM (2016) Estuarine fouling communities are dominated by nonindigenous species in the presence of an invasive crab. *Biol Invasions* 18:1653–1665

- Freites L, Himmelman JH, Lodeiros CJ (2000) Impact of predation by gastropods and crabs recruiting onto culture enclosures on the survival of the scallop *Euvola ziczac* (L.) in suspended culture. *J Exp Mar Bio Ecol* 244:297–303
- Gerard VA, Cerrato RM, Larson AA (1999) Potential impacts of a western Pacific grapsid crab on intertidal communities of the northwestern Atlantic Ocean. *Biol Invasions* 1:353–361
- Grabowski JH, Hughes AR, Kimbro DL (2008) Habitat complexity influences cascading effects of multiple predators. *Ecology* 89:3413–22
- Grason EW, Miner BG (2012) Behavioral plasticity in an invaded system: non-native whelks recognize risk from native crabs. *Oecologia* 169:105–115
- Gregory GJ, Quijón P a. (2011) The impact of a coastal invasive predator on infaunal communities: Assessing the roles of density and a native counterpart. *J Sea Res* 66:181–186
- Griffen BD (2006) Detecting emergent effects of multiple predator species. *Oecologia* 148:702–709
- Griffen BD, Byers JE (2006) Partitioning mechanisms of predator interference in different habitats. *Oecologia* 146:608–614
- Griffen BD, Williamson T (2008) Influence of predator density on nonindependent effects of multiple predator species. *Oecologia* 155:151–159
- Griffin JN, de la Haye KL, Hawkins SJ, Thompson RC, Jenkins SR (2008) Predator diversity and ecosystem functioning: Density modifies the effect of resource partitioning. *Ecology* 89:298–305
- Grosholz E, Ruiz G (1995) Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Mar Biol* 122:239–247
- Grosholz E, Ruiz G, Dean C, Shirley K, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. *Ecology* 81:1206–1224
- Haarr ML, Rochette R (2012) The effect of geographic origin on interactions between adult invasive green crabs *Carcinus maenas* and juvenile American lobsters *Homarus americanus* in Atlantic Canada. *J Exp Mar Bio Ecol* 422-423:88–100
- Haddon M, Wear RG, Packer HA (1987) Depth and density of burial by the bivalve *Paphies ventricosa* as refuges from predation by the crab *Ovalipes catharus*. *Mar Biol* 94:25–30
- Hall SJ, Raffaelli D, Robertson MR, Basford DJ (1990) The role of the predatory crab, *Liocarcinus depurator*, in a marine food web. *J Anim Ecol* 59:421–438
- Harding APC, Scheibling RE (2015) Feed or flee: Effect of a predation-risk cue on sea urchin foraging activity. *J Exp Mar Bio Ecol* 466:59–69
- Harris LG, Jones AC (2005) Temperature, herbivory and epibiont acquisition as factors controlling the distribution and ecological role of an invasive seaweed. *Biol Invasions* 7:913–924
- Hay ME, Pawlik JR, Duffy JE, Fenical W (1989) Seaweed-herbivore-predator interactions: Host-plant specialization reduces predation on small herbivores. *Oecologia* 81:418–427
- Hoffman JA, Katz J, Bertness MD (1984) Fiddler crab deposit-feeding and meiofaunal abundance in salt marsh habitats. *J Exp Mar Bio Ecol* 82:161–174
- Holdredge C, Bertness MD, Altieri AH (2008) Role of crab herbivory in die-off of New England salt marshes. *Conserv Biol* 23:672–9
- Hollebone AL, Hay ME (2007) Propagule pressure of an invasive crab overwhelms native biotic resistance. *Mar Ecol Prog Ser* 342:191–196
- Hollebone AL, Hay ME (2008) An invasive crab alters interaction webs in a marine community. *Biol Invasions* 10:347–358
- Hughes AR (2012) A neighboring plant species creates associational refuge for consumer and host. *Ecology* 93:1411–1420
- Hughes AR, Grabowski JH (2006) Habitat context influences predator interference interactions and the strength of resource partitioning. *Oecologia* 149:256–264
- Hunt HL, Mullineaux LS (2002) The roles of predation and postlarval transport in recruitment of the soft shell clam (*Mya arenaria*). *Limnol Oceanogr* 47:151–164
- Iribarne O, Armstrong D, Fernández M (1995) Environmental impact of intertidal juvenile Dungeness crab

- habitat enhancement: effects on bivalves and crab foraging rate. *J Exp Mar Bio Ecol* 192:173–194
- Kamenos NA, Moore PG, Hall-Spencer JM (2004) Maerl grounds provide both refuge and high growth potential for juvenile queen scallops (*Aequipecten opercularis* L.). *J Exp Mar Bio Ecol* 313:241–254
- Kamermans P, Blankendaal M, Perdon J (2009) Predation of shore crabs (*Carcinus maenas* (L.)) and starfish (*Asterias rubens* L.) on blue mussel (*Mytilus edulis* L.) seed from wild sources and spat collectors. *Aquaculture* 290:256–262
- Kimbro DL (2012) Tidal regime dictates the cascading consumptive and nonconsumptive effects of multiple predators on a marsh plant. *Ecology* 93:334–44
- Kimbro DL, Grosholz ED, Baukus AJ, Nesbitt NJ, Travis NM, Attioe S, Coleman-Hulbert C (2009) Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. *Oecologia* 160:563–575
- Kneib R, Weeks C (1990) Intertidal distribution and feeding habits of the mud crab, *Eurytium limosum*. *Estuaries* 13:462–468
- Knights AM, Firth LB, Walters K (2012) Interactions between multiple recruitment drivers: Post-settlement predation mortality and flow-mediated recruitment. *PLoS One* 7:e35096
- Kulp RE, Politano V, Lane HA, Lombardi SA, Paynter KT (2011) Predation of juvenile *Crassostrea virginica* by two species of mud crabs found in the Chesapeake Bay. *J Shellfish Res* 30:261–266
- Kwan CK, Sanford E, Long J (2015) Copper pollution increases the relative importance of predation risk in an aquatic food web. *PLoS One* 10:1–13
- Large SI, Smee DL (2013) Biogeographic variation in behavioral and morphological responses to predation risk. *Oecologia* 171:961–9
- Large SI, Torres P, Smee DL (2012) Behavior and morphology of *Nucella lapillus* influenced by predator type and predator diet. *Aquat Biol* 16:189–196
- Lipcius RN, Hines AH (1986) Variable functional responses of a marine predator in dissimilar homogenous microhabitats. *Ecology* 67:1361–1371
- Lohrer AM, Whitlatch RB (2002a) Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. *Mar Ecol Prog Ser* 227:135–144
- Lohrer AM, Whitlatch RB (2002b) Interactions among aliens: Apparent replacement of one exotic species by another. *Ecology* 83:719–732
- Lynch BR, Rochette R (2009) Spatial overlap and interaction between sub-adult American lobsters, *Homarus americanus*, and the invasive European green crab *Carcinus maenas*. *J Exp Mar Bio Ecol* 369:127–135
- Manríquez PH, Jara ME, Opitz T, Castilla JC, Lagos NA (2013) Effects of predation risk on survival, behaviour and morphological traits of small juveniles of *Concholepas concholepas* (loco). *Mar Ecol Prog Ser* 472:169–183
- Matassa CM, Trussell GC (2011) Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. *Ecology* 92:2258–66
- Matassa CM, Donelan SC, Luttbeg B, Trussell GC (2016) Resource levels and prey state influence antipredator behavior and the strength of nonconsumptive predator effects. *Oikos* 125:1478–1488
- McDonald PS, Jensen GC, Armstrong DA (2001) The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *J Exp Mar Bio Ecol* 258:39–54
- McKay, Kelly M, Heck Jr. KL (2008) Presence of the Jonah crab *Cancer borealis* significantly reduces kelp consumption by the green sea urchin *Strongylocentrotus droebachiensis*. *Mar Ecol Prog Ser* 356:295–298
- Mendonça V, Vinagre C, Boaventura D, Cabral H, Silva ACF (2016) Chitons' apparent camouflage does not reduce predation by green crabs *Carcinus maenas*. *Mar Biol Res* 12:125–132
- Micheli F, Peterson CH (1999) Estuarine vegetated habitats as corridors for predator movements. *Conserv Biol* 13:869–881
- Miron, G., Landry, T., MacNair NG (2002) Predation potential by various epibenthic organisms on commercial bivalve species in Prince Edward Island: Preliminary Results. *Can Tech Rep Fish Aquat Sci* 2392:44
- Mistri M (2003) Foraging behaviour and mutual interference in the Mediterranean shore crab, *Carcinus*

- aestuarii*, preying upon the immigrant mussel *Musculista senhousia*. Estuar Coast Shelf Sci 56:155–159
- Mistri M (2004) Predatory behavior and preference of a successful invader, the mud crab *Dyspanopeus sayi* (Panopeidae), on its bivalve prey. J Exp Mar Bio Ecol 312:385–398
- Miyashita LK, Richardson JP, Duffy JE (2016) Effects of predator richness and habitat heterogeneity on prey suppression in an estuarine food chain. Mar Ecol Prog Ser 559:13–20
- Molis M, Preuss I, Firmenich A, Ellrich J (2011) Predation risk indirectly enhances survival of seaweed recruits but not intraspecific competition in an intermediate herbivore species. J Ecol 99:807–817
- Munari C, Mistri M (2012) Short-term sublethal hypoxia affects a predator-prey system in northern Adriatic transitional waters. Estuar Coast Shelf Sci 97:136–140
- Navarrete SA, Castilla JC (2003) Experimental determination of predation intensity in an intertidal predator guild: Dominant versus subordinate prey. Oikos 100:251–262
- Nelson WG (1981) Experimental studies of decapod and fish predation on seagrass macrobenthos. Mar Ecol Prog Ser 5:141–149
- Newsom AJ, Williams SL (2014) Predation and functional responses of *Carcinus maenas* and *Cancer magister* in the presence of the introduced cephalaspidean *Philine orientalis*. Estuaries and Coasts 37:1284–1294
- O'Connor NE, Emmerson MC, Crowe TP, Donohue I (2013) Distinguishing between direct and indirect effects of predators in complex ecosystems. J Anim Ecol 5:438–448
- O'Connor NE, Grabowski JH, Ladwig LM, Bruno JF (2008) Simulated predator extinctions: Predator identity affects survival and recruitment of oysters. Ecology 89:428–38
- Olafsson E, Ndaro S (1997) Impact of the mangrove crabs *Uca annulipes* and *Dotilla fenestrata* on meiobenthos. Mar Ecol Prog Ser 158:225–231
- Powers SP, Kittinger JN (2002) Hydrodynamic mediation of predator–prey interactions: Differential patterns of prey susceptibility and predator success explained by variation in water flow. J Exp Mar Bio Ecol 273:171–187
- Premo KM, Tyler AC (2013) Threat of predation alters the ability of benthic invertebrates to modify sediment biogeochemistry and benthic microalgal abundance. Mar Ecol Prog Ser 494:29–39
- Quinn B, Boudreau M, Hamilton D (2012) Inter- and intraspecific interactions among green crabs (*Carcinus maenas*) and whelks (*Nucella lapillus*) foraging on blue mussels (*Mytilus edulis*). J Exp Mar Bio Ecol 412:117–125
- Raffaelli D, Conacher A, McLachlan H, Emes C (1989) The role of epibenthic crustacean predators in an estuarine food web. Estuar Coast Shelf Sci 28:149–160
- Ray-Culp M, Davis M, Stoner AW (1999) Predation by xanthid crabs on early post-settlement gastropods: the role of prey size, prey density, and habitat complexity. J Exp Mar Bio Ecol 240:303–321
- Reinsel K a. (2004) Impact of fiddler crab foraging and tidal inundation on an intertidal sandflat: Season-dependent effects in one tidal cycle. J Exp Mar Bio Ecol 313:1–17
- Reynolds PL, Bruno JF (2013) Multiple predator species alter prey behavior, population growth, and a trophic cascade in a model estuarine food web. Ecol Monogr 83:119–132
- Richards MG, Huxham M, Bryant A (1999) Predation: A causal mechanism for variability in intertidal bivalve populations. J Exp Mar Bio Ecol 241:159–177
- Ross DJ, Johnson CR, Hewitt CL, Ruiz GM (2004) Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. Mar Biol 144:747–756
- Schmitt RJ, Holbrook SJ, Brooks AJ, Lape JCP (2009) Intraguild predation in a structured habitat: Distinguishing multiple-predator effects from competitor effects. Ecology 90:2434–43
- Schneider FI, Mann KH (1991) Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape, epiphyte cover and predation. J Exp Mar Bio Ecol 145:119–139
- Scyphers SB, Powers SP (2013) Context-dependent effects of a marine ecosystem engineer on predator-prey interactions. Mar Ecol Prog Ser 491:295–301
- Siddon CE, Witman JD (2004) Behavioral indirect interactions: Multiple predator effects and prey switching in the rocky subtidal. Ecology 85:2938–2945

- Silliman BR, Layman CA, Geyer K, Zieman JC (2004) Predation by the black-clawed mud crab, *Panopeus herbstii*, in Mid-Atlantic salt marshes: Further evidence for top-down control of marsh grass production. *Estuaries* 27:188–196
- Spivak AC, Canuel EA, Duffy JE, Richardson JP (2007) Top-down and bottom-up controls on sediment organic matter composition in an experimental seagrass ecosystem. *Limnol Oceanogr* 52:2595–2607
- Sponaugle S, Lawton P (1990) Portunid crab predation on juvenile hard clams: Effects of substrate type and prey density. *Mar Ecol Prog Ser* 67:43–53
- Stachowicz JJ (1998) The ecology and evolution of defensive associations: Complex interactions between crabs, corals, and seaweeds. University of North Carolina at Chapel Hill
- Stachowicz JJ, Hay ME (1999) Mutualism and coral persistence: The role of herbivore resistance to algal chemical defense. *Ecology* 80:2085–2101
- Stickle WB, Wyler HJ, Dietz TH (2007) Effects of salinity on the juvenile crab physiology and agonistic interactions between two species of blue crabs, *Callinectes sapidus* and *C. similis* from coastal Louisiana. *J Exp Mar Bio Ecol* 352:361–370
- Tan EBP, Beal BF (2015) Interactions between the invasive European green crab, *Carcinus maenas* (L.), and juveniles of the soft-shell clam, *Mya arenaria* L., in eastern Maine, USA. *J Exp Mar Bio Ecol* 462:62–73
- Trussell GC, Ewanchuk PJ, Bertness MD (2002) Field evidence of trait-mediated indirect interactions in a rocky intertidal food web. *Ecol Lett* 5:241–245
- Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. *Ecology* 84:629–640
- Trussell GC, Ewanchuk PJ, Bertness MD, Silliman BR (2004) Trophic cascades in rocky shore tide pools: distinguishing lethal and nonlethal effects. *Oecologia* 139:427–32
- Trussell GC, Ewanchuk PJ, Matassa CM (2006) Habitat effects on the relative importance of trait- and density-mediated indirect interactions. *Ecol Lett* 9:1245–52
- Trussell GC, Ewanchuk PJ, Matassa CM (2008) Resource identity modifies the influence of predation risk on ecosystem function. *Ecology* 89:2798–807
- Tyrrell MC, Guarino PA, Harris LG (2006) Predatory impacts of two introduced crab species: Inferences from microcosms. *Northeast Nat* 13:375–390
- Valinoti CE, Ho C-K, Armitage AR (2011) Native and exotic submerged aquatic vegetation provide different nutritional and refuge values for macroinvertebrates. *J Exp Mar Bio Ecol* 409:42–47
- Vinueza LR, Branch GM, Branch ML, Bustamante RH (2006) Top-down herbivory and bottom-up El Niño effects on Galápagos rocky-shore communities. *Ecol Monogr* 76:111–131
- Virnstein RW (1977) The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58:1200–1217
- Walton WC, MacKinnon C, Rodriguez LF, Proctor C, Ruiz GM (2002) Effect of an invasive crab upon a marine fishery: green crab, *Carcinus maenas*, predation upon a venerid clam, *Katelysia scalarina*, in Tasmania (Australia). *J Exp Mar Bio Ecol* 272:171–189
- West DL, Williams AH (1986) Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *J Exp Mar Bio Ecol* 100:75–95
- Whitlow WL (2010) Changes in survivorship, behavior, and morphology in native soft-shell clams induced by invasive green crab predators. *Mar Ecol* 31:418–430
- Wong MC, d'Entremont J, Barbeau MA (2012) An approach for quantifying effects of multiple predators that forage on different time scales. *J Exp Mar Bio Ecol* 420–421:100–109
- Woodin SA (1981) Disturbance and community structure in a shallow water sand flat. *Ecology* 62:1052–1066